The Landdroskop area in the Hottentots Holland Mountains as a refugium for melanistic lizard species: an analysis for conservation.

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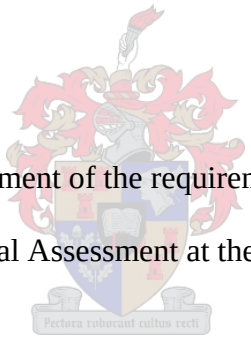

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DECLARATION

I the undersigned hereby declare that the work contained in this thesis is my own original work and has not previously in its entirety or part been submitted at any university for a degree.

Signature…… Date……

ABSTRACT

The Dwarf Crag Lizard, *Pseudocordylus nebulosus*, is one of several relict ectotherm species associated with the mistbelt of the Cape folded mountain belt. Prior to this study, it was only known from a single locality in the Hottentots Holland Mountains. In this study, the distribution range and microhabitat preferences of *P. nebulosus* were determined and resource partitioning among the three melanistic cordylids (*C. oelofseni*, *P. capensis* and *P. nebulosus*), co-occurring in this area, investigated. Using the locality where *P. nebulosus* was first discovered as centerpoint, surveys were conducted in all directions and the occurrence of all three melanistic species recorded. The previous known range of *P. nebulosus*, of only 0.04 km^2, was extended to 11 km^2. Of the three melanistic cordylids, *P. nebulosus* has by far the smallest range, completely overlapping with the ranges of both the other two melanistic cordylids. *Pseudocordylus nebulosus* was found to show a distinct affinity for water bodies such as mountain streams and seepage areas. Distinct differences in resource partitioning were found among the three species regarding crevice selection, which will prevent any significant competition during periods of environmental stress. *Cordylus oelofseni* preferred small crevices at ground level, *P. capensis* preferred large rock structures high above ground level and *P. nebulosus* utilized intermediate sized rock structures. Because of its relatively small range and melanistic colour, *P. nebulosus* could be a key indicator species of environmental change. Although the lack of objective fire management and global warming may be immediate threats to the survival of this species, possible illegal collection due to the easy access via the popular hiking trail in the area, is probably less significant a threat than was previously thought. Although its known range has been extended considerably, it is recommended that the *Vulnerable* status of *P. nebulosus* be maintained. This study

provides baseline data that could be useful in future monitoring programmes to predict declines and fluctuations.

In the second part of this study, the aim is to provide information about sexual dimorphism in *P. nebulosus* and to discuss the observed variation in sexual size dimorphism among montane cordylids. Data were recorded for all *P. nebulosus* individuals encountered in the Landdroskop area (Hottentots Holland Mountains), irrespective of size and sex. The total sample of 87 lizards recorded, consisted of 26 adult males, 49 adult females and 12 indeterminates. Size at sexual maturity was determined at 60 mm snout-vent length (SVL) for both sexes. The highly female-biased adult sex ratio recorded for *P. nebulosus*, is considered to be due to sampling error, gravid females probably basking more than males, making them easier to locate during searches. Generation glands were found to be present in males only and the number present was significantly correlated to body size. Both adult males and adult females possessed active femoral glands, but males had significantly more than females. Females were found to reach larger body sizes than males, but adult males had relatively larger heads than females. No significant difference in scar frequency was found between the male and female samples. Variation in sexual size dimorphism among montane cordylids is discussed and the need for more comprehensive data pointed out. The female-biased sexual size dimorphism in *P. nebulosus* and its sister species, *P. capensis*, is tentatively ascribed to fecundity selection for offspring to be large at birth in order to survive in a predictable unfavourable environment at high altitudes. Sexual dimorphism in head size is ascribed to sexual selection, males probably being territorial as in many other cordylids.

UITTREKSEL

Die Dwerg Kransakkedis (Wolkakkedis), *Pseudocordylus nebulosus*, is een van vele reliek ektototerm spesies wat met die misgordel van die Kaapse Plooiberge geassosieer word. Voor die aanvang van hierdie studie was hierdie akkedis slegs van een enkele lokaliteit in the Hottentots-Hollandberge bekend. In hierdie studie is die verspreidingsarea en mikrohabitatvoorkeure van *P. nebulosus* vasgestel en hulpbron/habitat verdeling tussen die drie melanistiese gordelakkedisse (*C. oelofseni*, *P. capensis* en *P. nebulosus*) wat simpatries in die area voorkom, is ondersoek. Deur die lokaliteit waar *P. nebulosus* eerste ontdek is as vertrekpunt te gebruik, is soektogte in die omliggende area onderneem en die voorkoms van al drie melanistiese spesies aangeteken. *Pseudocordylus nebulosus* se voorheen bekende verspreidingsarea van net 0.04 km^2 is vergroot tot 11 km^2. *Pseudocordylus nebulosus* het deurgaans in verspreiding met die ander twee melanistiese gordelakkedisse oorvleuel en ook verreweg die kleinste verspreidingsarea van die drie gehad. Daar is gevind dat *P. nebulosus* ‘n duidelike affiniteit vir waterbronne soos bergstroompies en sypelareas toon. Duidelike verskille in hulpbron/mikrohabitatvoorkeure wat die keuse van skeure aanbetref, is tussen die drie spesies gevind. Dit sal waarskynlik enige betekenisvolle kompetisie tussen die drie melanistiese spesies tydens ongunstige tye verhoed. *Cordylus oelofseni* het klein skeure op grondvlak verkies, terwyl *P. capensis* groot rotsstrukture hoog bo grondvlak verkies het en *P. nebulosus* intermediêre rotsstrukture. As gevolg van die spesie se relatiewe klein verspreidingsarea sowel as melanistiese kleur, kan *P. nebulosus* ‘n sleutelspesie wees in navorsing oor omgewingsverandering. Alhoewel die afwesigheid van doelgerigte brandbestuur en globale verwarming onmiddelike gevare vir die oorlewing van die spesie inhou, is die moontlikheid van onwettige versameling a.g.v die maklike toegang d.m.v ‘n populêre

staproete, waarskynlik nie so ‘n groot gevaar soos wat voorheen gevrees is nie. Alhoewel die verspreidingsarea van *P. nebulosus* nou aansienlik vergroot is, word aanbeveel dat die status van *Kwesbaar* behou word. Hierdie studie verskaf basiese inligting vir die gebruik tydens moniteringsprogramme om afnames en fluktuasies in die toekoms te kan voorspel.

Die doel van die tweede deel van hierdie studie is om inligting oor seksuele dimorfisme by *P. nebulosus* te verskaf en om die variasie in seksuele dimorfisme by bergvorme van die familie te bespreek. Data is ingesamel vir alle *P. nebulosus* individue wat in die Landdroskop area (Hottentots-Hollandberge) raakgeloop is, ongeag grootte en geslag. Die totale monster van 87 akkedisse het bestaan uit 26 volwasse mannetjies, 49 volwasse wyfies, en 12 individue van onbepaalbare geslag. Die grootte waarby geslagsrypheid bereik word is vasgestel as 60 mm SVL (snoet-kloaak-lengte) vir beide geslagte. Die volwasse geslagsverhouding vir *P. nebulosus*, wat sterk ten gunste van wyfies was, kan toegeskryf word aan onakkurate data insameling, aangesien dragtige wyfies waarskynlik meer as mannetjies in die son bak en daarom makliker was om op te spoor tydens soektogte. Slegs mannetjies besit generasiekliere en daar is gevind dat die hoeveelheid kliere merkbaar met liggaamsgrootte gekorreleer is. Beide volwasse mannetjies en volwasse wyfies het aktiewe femorale kliere, maar mannetjies het merkbaar meer as wyfies. Daar is gevind dat wyfies groter liggaamsgroottes as mannetjies bereik, maar dat volwasse mannetjies relatief groter koppe as wyfies het. Geen merkbare verskille is gevind tussen mannetjies en wyfies wat die frekwensie van beserings betref nie. Variasie in seksuele dimorfisme by bergvorme is bespreek en die behoefte aan omvattende data is uitgewys. Die seksuele dimorfisme ten opsigte van liggaamsgrootte ten gunste van wyfies in *P. nebulosus* en sy susterspesie, *P. capensis*, is tentatief toegeskryf aan

seleksie vir fekunditeit om groter kleintjies te hê wat in ‘n voorspelbaar ongunstige omgewing by hoë hoogtes kan oorleef. Seksuele dimorfisme in kopgrootte is toegeskryf aan seksuele seleksie waar mannetjies waarskynlik territoriaal is, soos die geval is by baie ander Cordylidae spesies.

The Dwarf Crag Lizard, *Pseudocordylus nebulosus*

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DEDICATION

I dedicate this thesis to my Mother.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 The Cape Floristic Region

The Cape Floristic Region (CFR), which is synonymous in distribution to the Fynbos Biome (Cowling, 1992), is considered to be one of the 25 biodiversity hotspots of the world (Myer *et al*., 2000). The CFR stretches along the coastal mountains and plains of South Africa from Nieuwoudtville in the west to Port Elizabeth in the east and covers less than 0.04% of the entire land surface of the earth. It is also the only floral kingdom found entirely within one country. The region has an extraordinarily high diversity per unit area and has an incredible botanical wealth, encompassing approximately 8 500 species. In an attempt to effectively conserve the natural environment and biodiversity of the CFR, the Cape Action for People and the Environment (CAPE) was established in 2000. The CAPE strategy has the following aims: Conserving biodiversity in priority areas, using resources sustainably, and strengthening institutions and governance (CAPE, 2000). CAPE is the first conservation strategy of its kind developed for an entire biodiversity hotspot.

The CFR is especially rich in herpetofauna with a high degree of endemism. Twenty four of the 44 frog species and 38 of the 145 reptile species occurring in the CFR are endemic (Baard & De Villiers, 2000). The herpetofauna of the CFR is poorly studied, largely because of the inaccessibility of parts of the Cape Fold Mountains. The majority of lizard species in the CFR are rupicolous (Branch, 1998) and the extensive mountains in the area probably support a rich lizard fauna. New reptile and amphibian species are still being discovered on a regular basis (Channing

& Hendricks, 1994; Mouton & Van Wyk, 1995; Haacke, 1996; Dawood & Channing, 2000), showing that the mountains are in urgent need of more detailed surveys.

1.2 Conservation

All lizards in the Western Cape are currently classified as Protected Wild Animals (Schedule 2) by the Nature Conservation Ordinance (No. 19 of 1974). There are, however, still constraints towards the conservation of herpetofaunal diversity in the CFR. The localised distribution and low mobility of many frog and lizard species make them extremely vulnerable to environmental change. Habitat degradation and destruction due to urban and agricultural development (especially in the lowlands of the south-west Western Cape), and the spread of invasive alien vegetation are the most important factors in the deteriorating conservation status of many taxa (Baard *et al.*, 1999). *In situ* habitat conservation strategies form the single most important aspect in securing the survival of many taxa and are therefore crucially important to target lowland sites in need of protection and mitigation against habitat disturbance and degradation (Baard *et al.*, 1999).

Current conservation of the CFR herpetological resource is unintentionally biased towards montane species because of the hostility of the mountainous terrain and the vast network of mountain reserves and catchment areas (Baard *et al*., 1999). While the reptiles and amphibians in montane habitats seem to be well conserved by the current CFR reserve system, there is still a definite need to manage these habitats properly in an effort to maintain the unique species assemblages.

1.3 Possible threats

1.3.1 Illegal collection

The herpetofauna of the montane regions of the Fynbos Biome are in danger of potential collection for illegal trade, an increasing problem (Baard & De Villiers, 2000). More attention is currently being turned towards South Africa, because of the dwindling supply from over-exploited countries, e.g., 627 718 wild-caught ball pythons, *Python regius,* and 10 039 wild-caught pancake tortoises, *Malacochersus tornieri,* were imported into the USA from Africa during 1983-1995 (Hoover, 1998). The national Department of Environmental Affairs & Tourism is currently responsible for the conservation of biodiversity in South Africa. By signing the Convention on Biodiversity and the CITES convention, the South African Government has pledged itself towards biodiversity conservation and the control of illegal trade. There is, however, a problem with enforcing the legislation that is in place, thus seriously hampering effective conservation of the CFR herpetofauna (Baard *et al.*, 1999).

1.3.2 Fire

On average, most fynbos plant communities burn every 12 to 15 years (Cowling & Richardson, 1995). Fire is critically important in the regeneration of fynbos (Richardson *et al*., 1994), but frequent fires are, however, undesirable. Veldfires in mountain areas have the potential to alter habitats crucial to the survival of certain montane species (Baard & De Villiers, 2000).

Although the role of fire in the Fynbos Biome has been intensively studied, little is known about the effect of fire on animals, particularly lower vertebrates and invertebrates. Unlike birds and mammals, most lower vertebrates have low mobility. Escape from a fire front by flight, emigration from an adverse post-fire environment,

and immigration to recolonise burnt areas, may therefore be highly ineffective. The potential direct and indirect effects of fire are anticipated to be much more severe for lower vertebrates than for birds and mammals. Besides the direct impact of lowering populations to a critical threshold of survival, populations may be unable to recover after fire because of lower recruitment and inadequate corridors to facilitate recolonisation. If not managed correctly, fires could change vegetation cover in the medium to long term, which in turn may affect run-off and destroy seepage, sponge and other damp areas which may be important to the survival of taxa dependent on these habitats (Baard & De Villiers, 2000). There is thus a definite need to manage fire in mountain habitats properly if the unique montane species assemblages are to be maintained.

In a study on the effects of fire on rock-dwelling lizards, Baard *et al*. (unpublished data) found that a population of the rupicolous *Agama atra atra* remained relatively stable after a fire, but did record lizards with burnt tails and feet. They also mentioned that in an area where there were fewer rocks for shelter there was a higher mortality of *A. a. atra.* It would thus appear that rocky environments offer protection against fire and that rupicolous lizard species are able to survive most fires due to their preference for rocky habitats.

Baard (1990) suggests that fires may also have secondary effects on animals. These include depletion of cover leading to increased predation as well as decreased prey availability. As rupicolous lizards do not rely to a large extent on concealment by vegetation, this factor would probably be insignificant for them. Most of the lizard species occurring in the CFR are heliothermic baskers and thus prefer as much sunlight as possible. Theoretically, as soon as the vegetation becomes too dense and high, lizards will not be able to obtain enough sunlight and thus not be able to survive.

Regular fires are thus thought to be needed to control the height and density of the vegetation (Baard, 1990).

1.3.3 Alien vegetation

Substantial parts of the CFR are already under moderate to dense infestation by invasive alien plants, e.g. *Acacia*, *Eucalyptus*, *Hakea*, *Pinus* and *Sesbania* (Shroyer *et al*., 1998). Invasion by alien plant species has already resulted in the extinction of 26 plant species in the region and many other plant species are currently at risk (Bond *et al*., 1992). Alien plants thus have the potential to change the habitat structure of many areas. Most of these alien invasive species occur in the form of tall shrubs (*Acacia*, *Hakea*) or trees (*Eucalyptus*, *Pinus*), thus casting large amounts of shade. Because heliothermic baskers are dependent on sunlight for thermoregulation, these shaded areas would be extremely unsuitable and thus limit the amount of habitat available for lizard species of the CFR. Alien infestation can also lead to much hotter fires through increasing biomass that are detrimental even to some of the fire-loving Fynbos species (Brooks *et al*., 2004).

1.3.4 Global climate change

In the last 150 years carbon dioxide levels have increased by more than 35% contributing to the so-called ‘greenhouse effect’. The projected impact of accelerating global climate change on particularly the western half of South Africa, and specifically the Cape Floral Kingdom, is predicted to be quite severe over the next 50-100 years (Midgley *et al*., 2001). The northern arm of the Fynbos Biome stretching up to Nieuwoudtville may disappear altogether (Midgley *et al*., 2001).

Global climate change may also have a number of secondary effects, e.g. fires may become more frequent and extensive as the climate becomes hotter and drier. Climate change together with the increasing levels of carbon dioxide in the atmosphere may also encourage the growth of woody alien plants in the Fynbos Biome (Midgley *et al*., 2001).

It is believed that the phenomenon of global climate change could potentially be responsible for the ultimate local extinction of at least some of the highly specialised and threatened frogs and lizards of the CFR. Global warming probably holds particular threats to mistbelt-adapted species that are already restricted to cool enclaves, many of which will disappear with global warming.

Predictions have been made that species should respond to climate change according to their distributions along climatic gradients, this has been supported by studies on the changes in bird abundance at 1 540 m on a Costa Rican tropical mountain where recolonisation of birds from lower down the mountain side to higher elevations was observed (Pounds *et al*., 1999). While some species may move to higher elevations to escape the increasing temperatures, species at the highest elevations have nowhere further to move to and may subsequently face extinction as habitat and resources become limited. This was found in a Costa Rican mist forest where two highland anoline lizard species, *Norops tropidolepis* and *N. altae* began to decline in the late 1980's and disappeared by 1996 due to the variation in rainfall brought about by global climate change (Pounds *et al.*, 1999). Few researchers have however directly assessed the effects of climate change on reptiles (Gibbons *et al*., 2000).

1.4 Melanistic species

One of the unique phenomena in the CFR is the distinct clustering of melanistic vertebrate and invertebrate species at the south-western corner of the Cape (Mouton, 1985, 1986; Mouton & Oelofsen, 1988; Mouton & Van Wyk, 1995). Generally, melanism is more common in the northern latitudes, in mountains, and on islands (Edelstam, 1976). Badenhorst (1990) demonstrated that the CFR melanistic cordylid populations seem to be cold-adapted, associated with conditions of limited solar radiation owing to a high incidence of fog or cloud cover. In this area, coastal melanistic populations are associated with zones of upwelling of cold water in the Atlantic Ocean, while montane melanistic populations occur at localities where there is a high incidence of orographic fog and cloud cover (Badenhorst *et al*., 1992). Therefore, melanistic cordylid populations generally have to contend with relatively exposed environmental conditions of low temperature and limited solar radiation due to the filtering effect of fog and cloud cover (Badenhorst, 1990). It is theorised that melanism in cordylid lizards, in areas of limited solar radiation, primarily serves a thermoregulatory function, although a cryptic function is also possible (Mouton & Van Wyk, 1992; Cordes & Mouton, 1995). The photoprotective proporties of melanin have been well documented, thus melanism could also serve as protection against harmful ultraviolet radiation (Kollias *et al*., 1991).

It is generally accepted that temperature plays an important role in the distribution of lizards (Poynton & Broadley, 1978). Mouton (1986a) established that, with the exception of a melanistic population of *Cordylus polyzonus* in the eastern Northern Cape Province and southern Free State, melanistic cordylids are restricted to the south-western coastal regions of the Western Cape Province. Melanistic species in this region include *Cordylus coeruleopunctatus, C. niger, C. oelofseni, C. peersi, C.*

polyzonus, *Pseudocordylus capensis* and *P. nebulosus*. The distribution of melanistic cordylid populations in the southern Western Cape is temperature correlated, with lizards being restricted to insular and peninsular situations and coastal rock (*C. niger* and *C. polyzonus*) and relatively high altitudes in the Cape Fold Mountains (*C. oelofseni*, *P. capensis* and *P. nebulosus*) (Badenhorst, 1990). Along the Cape Fold Mountains mean temperatures are drastically influenced by altitude, with higher altitudes normally being cooler (Badenhorst, 1990).

All current melanistic forms occur in the form of small isolated populations limited to cool enclaves, suggesting that they are presently in a contracted state under strong environmental pressure (Badenhorst, 1990). It also suggests that the adverse climatic conditions with which melanism is presently associated, occurred on a large scale in the south-western Cape in the past (Mouton & Van Wyk, 1995; Daniels *et al*., 2004). These melanistic species may thus be relicts of once larger melanistic populations (Mouton & Oelofsen, 1988; Daniels *et al*., 2004).

Mouton & Oelofsen (1988) proposed a model for the evolution of melanism in the *cordylus-niger-oelofseni* complex which suggests that during a glacial period, a western coastal population became isolated from an eastward retreating ancestral form. The western coastal lowland population became melanistic as an adaptation to conditions of limited sunshine during the glacial period. During subsequent amelioration of climates, the cold-adapted melanistic population fragmented into a coastal population, occurring from the Cape Peninsula to Saldanha in the north, and a montane population, occurring along the western section of the Cape Fold Mountains, from Landdroskop in the south to Piketberg in the north. These two populations later fragmented even further and the still warm-adapted, non-melanistic eastern population expanded its range into the western coastal lowlands into areas left vacant by the

retreating melanistic forms. Mouton & Oelofsen (1988) suggest that this climatic event also explains the high incidence of melanistic populations in the south western corner of the African subcontinent. According to an electrophoretic analysis done by Brody *et al*. (1993), the time of divergence of the taxa in the *cordylus-niger-oelofseni* group range from 1-3 million years ago. The most recent analysis, however, found that the divergence time was during the Miocene 17-15 million years ago (Daniels *et al*., 2004). Thus, melanism originated much earlier than was previously theorised and the current melanistic species of the Cape Fold Mountains may be up to 17 million years old. According to Daniels *et al*. (2004) the development of a cold water current and upwelling system along the southwest coast of Africa during the Miocene was instrumental in the evolution of melanism in this lizard clade and possibly also in other ectotherm clades with melanistic forms occurring in the area.

1.5 Hottentots Holland Mountains - Landdroskop

The Cape Fold Mountains are home to several relict species or populations of lower vertebrates and invertebrates, including several melanistic populations, associated with the mistbelt of these mountains. One such an area in the southern Western Cape containing isolated melanistic populations, is the Landdroskop area (34°02'S; 19°59'E), in the Hottentots Holland Mountains, about 1 200-1 500 m above sea-level. The area lies in the mistbelt which occupies the upper parts of these mountains. For at least a few hours of most days of the year, the mist is accompanied by rain or drizzle, ensuring cool and damp conditions (Sirgel, 1985). At Landdroskop at least three melanistic lizard species (*C. oelofseni, P. capensis, P. nebulosus*) and two melanistic slug species (*Ariopelta capensis* and *Ariostralis nebulosa*) co-occur within the mistbelt. The two slug species described by Sirgel (1985), occur at a site

near the top end of a narrow ravine, Landdroskloof, on the western slopes of the Hottentots Holland Mountains, within 500 m from where the melanistic lizard species occur. The characters of both slug species suggest that they should be regarded as relict primitive types (Sirgel, 1985).

There is a strong possibility that a stag beetle (*Colophon cameroni* or *C. stokoei*) also occurs at this locality. Both species have been reported to occur in the Hottentots Holland Mountains (Endrödy-Younga, 1988). They are recognized as representatives of a biome which evolved on the low-lying plainland during a period when the environmental conditions there were similar to those of the high altitudes to which they are restricted today (Endrödy-Younga, 1988). They have been referred to as mountain relicts (Endrödy-Younga, 1988).

Geertsema (pers. com.) furthermore collected melanistic larvae of an undescribed moth species of the genus *Psycharium* at Landdroskop. These specimens show, on superficial comparison with other larvae of *Psycharium* (Geertsema, 2000), highly interesting primitive features, the most interesting feature being the black colouration unknown in other members of the genus at lower altitudes.

The region also hosts an endemic new species of moss frog, *Arthroleptella landdrosia* (Dawood & Channing, 2000). This species is also very dark in colour, with a black ventral surface and vocal sac (Dawood & Channing, 2000). The presence of this and several other unique faunal species has warranted the listing of the greater Landdroskop area as a critical habitat by CapeNature (Baard & De Villiers, 2000).

The presence of numerous melanistic species from different animal taxa at one locality suggests that this locality acts as a refugium for remnants of unique cool- or mist-adapted fauna. Although many melanistic populations of single species are to be

found along the Cape Fold Mountains, the Landdroskop locality is the only montane refugium known thus far where several melanistic ectotherms co-occur. The cloudy, cool conditions, in which the melanistic species are found, possibly echo the conditions under which melanism first evolved (Mouton & Oelofsen, 1988). The Landdroskop locality is therefore the ideal one for studies on the functional and ecophysiological significance of melanism, as closely related melanistic and non-melanistic species (e.g. *Pseudocordylus microlepidotus*) co-occur here. There are also preliminary indications that melanistic forms can be valuable in studying the impact of the "greenhouse effect" and climate change on animal populations (Cordes & Mouton, 1995). The conservation of the Landdroskop ecosystem and its individual melanistic species is therefore of special importance.

To date, no attempt has been made to describe the physical and biotic attributes of the Landdroskop refugium or to identify other such refugia in the Cape Fold Mountains.

1.6 Pseudocordylus nebulosus

One of the recently discovered species at Landdroskop is the Dwarf Crag Lizard, *Pseudocordylus nebulosus* (Mouton & Van Wyk, 1995), a melanistic lizard occurring in an isolated population on the northern slopes. Its name, literally meaning cloudy or dark crag lizard, refers to its occurrence within the mistbelt of the Hottentots Holland Mountains, as well as its melanistic body colour (Mouton & Van Wyk, 1995). This species and its conservation is of particular importance as it is known only from this locality, an area of only a few hundred square meters near the mountain summit. There is a relatively large morphological gap between *P. nebulosus* and its closest relatives, *C. coeruleopunctatus* and *P. capensis*, indicating

that it is a relatively ancient species (Mouton & Van Wyk, 1995). *P. nebulosus* has been called a lizard "missing link" and is one of several relict species or populations of lower vertebrates associated with the mistbelt of the Hottentots Holland Mountains. These relict species are of immense scientific importance because of the evolutionary and biological information they hold.

Mouton (pers. comm.) conducted a preliminary survey to determine the boundaries of the *P. nebulosus* population at Landdroskop, but, despite this effort, the species is still only known from this single locality.

The Landdroskop area is traversed by a series of hiking trails and at the time of the first discovery of *P. nebulosus*, received up to 12 000 visitors per year (CapeNature, pers. comm.). One of the possible impacts on the survival of *P. nebulosus* is the relatively easy access due to the hiking trail system (Baard, *et al.*, 1999), which could easily lead to illegal collection of individuals. Two overnight huts are presently situated close to where *P. nebulosus* is known to occur, while one of the Landdroskop hiking trails leads straight through the site where it was first discovered.

Because *P. nebulosus* and *P. capensis* are sister species (Frost *et al*., 2001) it is possible that they may have similar microhabitat preferences and compete for resources. It has, however, been suggested that within lizard communities, competition may not be particularly common; more exactly, competition may not be a major force in lizard community structuring (Chase, 1996). Competition is also not a static interaction, but may vary temporally and spatially (Chase, 1996). Competition for resources may, however, become a problem at the Landdroskop locality if the predicted increase in global temperatures (Midgley *et al*., 2001) leads to an increase in density of the closely related species at the upper reaches of the refugium and habitat becomes limited.

There is a possibility that *P. nebulosus* may have a much wider distribution in the Cape folded mountain belt, similar to that of the other melanistic girdled lizard species, but that other isolated populations have not been discovered yet because of the inaccessibility of most high altitude localities. Mouton & Van Wyk (1995) are of the opinion that there may be at best only a few very small isolated unknown populations of the crag lizard present in the Hottentots Holland Mountains at suitable localities where its melanistic body colour is an advantage.

1.7 Significance and objectives of the study

Since its discovery in 1995, no further research has been done on *P. nebulosus*. There is thus no information on its distribution or biology. This study was done in collaboration with CapeNature and will provide some baseline information on the species, which is needed for suitable conservation plans and monitoring programmes.

The first objective of this study was to determine the current conservation status of *P. nebulosus* in the Hottentots Holland Mountains by determining its distribution range and microhabitat preferences. As there are three melanistic cordylids co-occurring in the study area, habitat partitioning was also investigated to determine whether competition for resources could possibly occur.

The second objective was to investigate sexual dimorphism in *P. nebulosus*. This would shed some light on the social structure of the species and the evolution of this phenomenon in the montane cordylids of Southern Africa.

1.8 Additional outcomes of the study

A comprehensive database containing distribution data, individual measurements and microhabitat measurements for *P. nebulosus* is to be compiled for Hottentots Holland Nature Conservation (HHNC). This will assist them in their action plan for the effective conservation of the herpetofauna of the area.

Through the surveys six field rangers from HHNC were trained to distinguish between the three melanistic cordylid species occurring in their reserve. This will enable them to identify lizards in the field and effectively monitor the different species.

CHAPTER 2

CONSERVATION STATUS OF THE DWARF CRAG LIZARD, *PSEUDOCORDYLUS NEBULOSUS*, FROM THE HOTTENTOTS HOLLAND MOUNTAINS, SOUTH AFRICA

2.1 INTRODUCTION

In 1995, the Dwarf Crag Lizard, *Pseudocordylus nebulosus*, was described from the Hottentots Holland Mountains in the Western Cape Province, South Africa (Mouton & Van Wyk, 1995) (Fig. 2.1). The specific epithet *nebulosus* literally means 'cloud' and refers to the occurrence of this melanistic lizard within the mistbelt of the Hottentots Holland Mountains. The discovery of this species was another addition to the already long list of melanistic vertebrate and invertebrate species concentrated at the south-western tip of South Africa (Mouton & Oelofsen, 1988; Daniels *et al*., 2004).

In a phylogenetic analysis of the family Cordylidae, Frost *et al*. (2001) demonstrated that both *Pseudocordylus* and *Chamaesaura* are embedded within *Cordylus* and suggested that the former two be included in the latter to obtain a monophyletic classification. To avoid nomenclatural problems, we, however, adhere to the original classification.

Pseudocordylus nebulosus was first discovered along a mountain stream on the northern slopes of Landdroskop, a peak in the Hottentots Holland Mountains (Mouton & Van Wyk, 1995). Co-occurring with two melanistic slug species (*Ariopelta capensi*s and *Ariostralis nebulosa*), a melanistic moth larvae (Genus *Psycharium*) and two other melanistic cordylids (*Cordylus oelofseni* and *Pseudocordylus capensis*) in the Landdroskop area, it further contributes to the

uniqueness of this locality as the only known locality in the Cape Floristic Region where several melanistic vertebrate as well as invertebrate species co-occur. At an altitude of 1 200-1 500 m, the area is characterised by a high incidence of orographic fog, especially during summer months when south-easterly winds are prevalent (Campbell, 1983; Sirgel, 1985; Badenhorst, 1990).

The melanistic cordylid lizards of the CFR appear to be cold-adapted, being associated with conditions of limited solar radiation. Coastal melanistic cordylid populations are associated with zones of upwelling of cold water in the Atlantic Ocean, while montane melanistic populations occur at localities where there is a high incidence of orographic fog and cloud cover (Badenhorst, 1990). Daniels *et al.* (2004) found that melanism in the *cordylus-niger-oelofseni* clade evolved during the Miocene epoch, 17 to 15 million years ago. These authors are of the opinion that the development of a cold water current and upwelling system along the south-west coast of southern Africa during this epoch was instrumental in the evolution of melanism in this lizard clade and possibly also in other ectotherm clades occurring in the area. The climatic conditions with which melanism is presently associated thus probably occurred on a large scale in the south-western region in the past and the melanistic species may have had a much wider distribution than at present. Extant melanistic populations are therefore probably relicts of once larger melanistic populations (Mouton & Oelofsen, 1988; Daniels *et al*., 2004). The Landdroskop area can thus be seen as a refugium for cold-adapted melanistic ectotherms.

Despite several searches during the past few years, *P. nebulosus* was, prior to this study, only known from the single locality cited by Mouton & Van Wyk (1995). Species with small distribution ranges are particularly vulnerable to the effects of environmental change (Root & Schneider, 2002) and it was for this reason that Baard

et al. (1999) suggested that *P. nebulosus* be placed in the *Vulnerable* category of the IUCN Red Data list. The fact that a very popular hiking trail passes through the only known, apparently small population of *P. nebulosus*, with a popular resting spot at the stream where the species was first discovered, was a matter of some concern. Commercial exploitation of CFR herpetofauna has increased considerably during recent years and it was feared that easy access to this population of *P. nebulosus* could easily lead to its extermination. Although rock-dwelling in nature and occurring in a montane habitat where it is not impacted on by threats associated with agriculture and urban development, it is, however, not safe from the threats of alien plant infestation, poor fire management, and global warming. *Pseudocordylus nebulosus* furthermore co-occurs with its sister species, *P. capensis* (Frost *et al*., 2001), at the Landdroskop locality and the possibility exists that under conditions of environmental stress, competition for resources between these two species may negatively impact on *P. nebulosus*.

The aims of this study were threefold, firstly to determine the distribution range of *P. nebulosus* in the Landdroskop area, secondly to characterise the preferred microhabitat of *P. nebulosus*, and thirdly, to investigate possible habitat partitioning among the three melanistic cordylid species (*C. oelofseni*, *P. capensis* and *P. nebulosus*) occurring at the Landdroskop locality. This information was then used to re-evaluate the conservation status of this little-known melanistic species.

2.2 MATERIALS AND METHODS

2.2.1 Distribution range

As a first approach, searches were conducted in four directions from the point where *P. nebulosus* was first discovered in 1995 (Fig. 2.2 and 2.3). Following the

mountain stream, searches were conducted up and down the mountain side, thoroughly searching the rocky areas along the stream banks for lizards. Then, following the Boland Hiking Trail, searches were conducted in the direction of the overnight huts (to the east) and in the direction of the Helderberg Basin lookout point (to the west) (Fig. 2.3). A second approach was to conduct a larger scale search for *P. nebulosus* in the Hottentots Holland Mountains. The Boland Hiking Trail was used to cover the widest possible area along the western section of the Hottentots Holland Mountains. The hiking trail was followed from the overnight hut in the directions of Jonkershoek (hereafter referred to as the Jonkershoek Trail) and Sir Lowry's Pass (hereafter referred to as the Moordenaarskop Trail), respectively (Figs. 2.2-2.5). Where possible, searches covered the area 50 to 100 m above and below the trail. A 14 km hike was also undertaken from the 1 182 m high peak, "Hans se kop", searching in the direction of Moordenaarskop to the Landdroskop overnight huts. In addition, a two-day hike was undertaken from the Helderberg Valley up the steep western face of the Hottentots Holland Mountains to the summit, searching for *P. nebulosus* on the way (Fig. 2.2). The jeep track from the Nuweberg Forestry Station to the overnight huts was used to access the mountain top from the south-east, and while driving, the area was always scanned visually for active melanistic lizards.

Distributional information was not only recorded for *P. nebulosus*, but also for *C. oelofseni* and *P. capensis*. Basking lizards were recorded and where possible crevices were searched for concealed lizards. Coordinates for each point locality were obtained using a handheld GPS. Searches took a total of 440 man hours, involving on average five fieldworkers at a time.

2.2.2 Microhabitat preferences

Habitat partitioning: To investigate habitat partitioning among the three species, the height above ground level at which individuals were observed, either basking or sheltering inside a crevice, was recorded for all three species. Data were analysed statistically by means of pairwise multiple comparison statistic using Dunn's method. Probability values (*P*) smaller than 0.05 were considered significant. Data analysis was done using the computer programmes *Statistica 6.0*™ and *SigmaStat 2.3*™ for Windows.

Vegetation structure: Even though the cordylids of the Cape Fold Mountains are rock-dwelling and thus not dependent upon vegetation composition and structure, vegetation still forms part of their habitat, providing shade and a source of prey. It can also be an indicator of the moisture content of an area.

To record the composition of the vegetation at each site, cover-abundance values were attributed following a modified Braun-Blanquet approach as in Barkman *et al*. (1964). This technique was introduced to the Fynbos Biome by Werger *et al*. (1972). Eleven plots of 5 x 10 m were selected in the survey area at sites where *P. nebulosus* individuals were recorded. This is a standard size used in numerous other studies in Sandstone Fynbos and could thus be used to relate the vegetation in the plots to other studies done in the area (Boucher, 1978; Sieben, 2003; Sieben *et al*., 2004). Following the Braun-Blanquet approach, the vegetation plots were taken from homogeneous stands of vegetation (Sieben, 2003). For each plot the following environmental measurements were recorded: aspect, slope, the number of vegetation strata, the height of each stratum, the percentage rock and estimated vegetation cover, and the distance to the nearest water source. Species lists were then compiled and compared to other studies done in the Western Cape to rate plots according to their

moisture status. Plots were rated using species assemblages instead of single species presence.

2.3 RESULTS

2.3.1 Distribution range

The area surveyed in the Hottentots Holland Mountains is depicted in Figure 2.2. The area stretched from "Wesselsgat" in the south to the peak, The Triplets (1 503 m), in the north and the Landdroskop overnight huts in the east. The western boundary of the area is formed by the west-facing edge of the Hottentots Holland Mountain range. East of the overnight huts, the area becomes drier and steadily drops in altitude towards the interior.

An intensive search of the type locality of *P. nebulosus*, i.e., along the banks of a fast flowing mountain stream and small waterfall (Fig. 2.2 and 2.3) revealed that this lizard is present up to ± 50 m above the hiking trail and up to ± 70 m below the trail. Along the hiking trail, individuals were found up to 60 m from the stream on the eastern side and up to 20 m from the stream on the western side. About 10 m east of the main stream there is a seepage area along which several lizards were recorded. A total of 40 individuals were recorded in close proximity to the main stream. Individuals were recorded on loose boulders in the stream bed and along the rocky banks. The concentration of individuals at this site will be referred to as the waterfall colony.

Along the hiking trail in the direction of the overnight huts, i.e. east of the waterfall colony, a single individual was recorded on a vertical cliff face underneath a seepage area (-34º 2.951'S; 19º 0.077'E).

West of the waterfall colony, only one individual was recorded over a stretch of approximately 400 m. The vegetation along this stretch on either side of the trail was dense, with stands of 1.5 m high *Euryops abrotanifolius*, interspersed with isolated rocks. The next concentration of individuals, stretching up to 30 m above the trail, was located next to a seepage area (-34º 2.869'S; 18º 59.390'E), a short distance before the Jonkershoek Trail turns northwards at the Helderberg Basin lookout point (Fig. 2.3). The site was characterised by a steep slope with vertical cliff faces and freestanding rocks. Immediately after the trail turns northwards, two individuals were recorded on a rock scree, consisting of large boulders up to 2 m in height.

For the next 500 m the trail follows an east-facing slope up to where it starts to ascend the steep scree in the direction of the Jonkershoek Valley. This area was relatively homogenous, consisting of seepage areas interspersed with large rocky outcrops. Lizards were found concentrated around these rocky outcrops, consisting of loose lying rocks and vertical cliff faces (Fig. 2.3).

For the next 2 km along the trail in the direction of Jonkershoek, lizards were observed basking on rock screes (Fig. 2.4). Screes are also associated with moist conditions, forming drainage lines and containing mosses and ferns. Along this stretch of the trail only ten individuals were recorded, apart from a small concentration around a stream, 160 m east of the trail. At this concentration, lizards were recorded on boulders in the stream bed and on the banks within 10 m of the stream.

The most northerly records for *P. nebulosus* were obtained around a stream, just south of the first peak of the Three Triplets (-34º 1.391'S; 18º 59.143'E). All individuals were recorded within 10 m of the stream. For the next 400 m only

Cordylus oelofseni and *P. capensis* individuals were recorded. After this point the trail drops down into the Jonkershoek Valley and becomes steadily lower in altitude.

Following the Sphinx Route in the direction of Nuweberg and then the secondary trail towards Moordenaarskop (Fig. 2.5), no *P. nebulosus* individuals were recorded for the first kilometer, even though searches stretched 50 m above and below the trail. The first individual on the Moordenaarskop Trail was recorded on a high vertical cliff face in a gully next to a stream. At approximately 120 m west of this point, several more individuals were recorded, again within 10 m of a stream. On the southern side of the trail, a vast marshy valley occurs, not containing suitable habitat for rock-dwelling lizards. Approximately 190 m from the small concentration one individual was recorded in a moist gully characteristic of a seepage area. For the next 460 m there were very few crevices available. Thereafter a small concentration of individuals was recorded, again within 10 m of a fast flowing stream. Here the vegetation was fairly high and dense and lizards were only found on the eastern bank in vertical crevices in a rock face overlooking the stream.

From this point on there was very little rock cover on either side of the trail. Here the terrain allowed for searches stretching 500 – 600 m below the trail. The terrain consisted of low growing Restionaceae interspersed with small rocky outcrops and large freestanding boulders. Individuals were recorded on the overhanging cliffs along the edge of a deep ravine, leading to “Wesselsgat”. Of these individuals, three were also recorded within 15 m of a stream. The rest of the lizards were recorded on rocky outcrops on the eastern side of the ravine called “Witwatervalletjies” leading down to “Wesselsgat” in the south.

A search from “Hans se Kop” in the south produced three *P. nebulosus* individuals along the southern slopes of Moordenaarskop (34º 05.746'S; 18º 58.757'E)

and two along the eastern slopes of Moordenaarskop. No *P. nebulosus* individuals were recorded on "Hans se Kop" itself. Previous searches on "Hans se Kop" also did not produce any *P. nebulosus* individuals (Oelofsen *et al*., 1987).

The transect from the Helderberg Valley up Sneeukopkloof (Fig. 2.4) revealed no lizards on the west facing mountain side. The first *P. nebulosus* individuals were recorded right at the summit at an altitude of 1 280 m on the western side of Landdrosnaald (34º 2.724'S; 18º 58.735'E). At no stage were melanistic cordylids were ever observed along the route from the Nuweberg Forestry Station up to the Landdroskop overnight huts.

The estimated range of *P. nebulosus*, based on the results of this survey, is presented in Figure 2.6. Given the fact that further north there is a sudden drop in altitude and a low incidence of orographic fog (pers. observ.), "The Triplets" probably form the northern range limit. The western limit of the range would be the western edge of the Hottentots Holland range, above an altitude of approximately 1 200 m. The eastern border of the range probably follows the 1 200 m contour line along the north-, east- and south-facing slopes immediately east of the range summit. The southern range limit is probably along the southern and eastern slopes of Moordenaarskop, as *P. nebulosus* was not recorded on "Hans se Kop" and further south-west there is a sharp drop in altitude. The estimated range size is 11 km^2.

Wherever *P. nebulosus* was recorded, *C. oelofseni* and *P. capensis* were also present. The latter two species, however, have a much wider distribution in the area, far beyond the estimated range of *P. nebulosus*.

2.3.2 Microhabitat preferences

Habitat partitioning: Based upon the height above ground level where lizards bask or shelter in a crevice, significant differences in microhabitat preferences were observed among *C. oelofseni*, *P. capensis* and *P. nebulosus* (Dunn's Multiple Pairwise Comparison: $P < 0.001$ for all pairwise comparisons; Table 2.1; Fig. 2.7). *Cordylus oelofseni* predominantly made use of rocks lower than 1 m, *P. nebulosus* showed a preference for medium-sized rocks, while *P. capensis* was often recorded on quite large boulders or in crevices high above ground level.

Of the 135 *P. nebulosus* individuals recorded, 117 (87%) were recorded within 10 meters of a water source, either a mountain stream or seepage area (Table 2.2). The other two melanistic cordylids showed no particular preference for moist areas as they were recorded over a wide range of habitat types.

Vegetation structure: The plant communities identified from the 11 plots were classified as dry, moist, wet and stream communities based upon the species assemblages. Of the 11 plots, three contained species characteristic of a dry community, one was a dry rock face, two were classified as moist, characteristic of a southern slope, three were classified as wet, indicating seepage areas, and two were stream communities. Species characteristic of moist areas, were identified as *Anthochortus crinalis*, *Erica hispidula* and *Villarsia capensis*. The species characteristic of wet seepage areas, were identified as *Anthochortus crinalis, Berzelia squarrosa, Chondropetalum mucronatum, Gnidia oppositifolia, Raspalia microphylla* and *Restio purpurascens*. For results of the vegetation analysis, see Appendix 2.1.

After comparison with previous vegetation studies done in the area, communities related to the sample plots were identified, with the following results:

- Plot 1 was related to community B4: *Tetraria capillacea – Restio subtilis* Short to Tall Closed Restioland as in Sieben *et al*. (2004).
- Plots 2 and 10 were related to community 3.2.4.1.4: Mixed ericoid and restioid Fynbos of the upper mesic slopes in Boucher (1978).
- Plots 3 and 7 were related to community A2: *Elegia thyrsifera – Centella eriantha* Short Closed Herbland in Sieben *et al*. (2004).
- Plots 4, 5 and 9 were related to community B2: *Erica autumnalis – Restio purparascens* Tall Closed Restioland in Sieben *et al*. (2004).
- Plot 6 was related to community A3: *Anthochortus crinalis – Elegia intermedia* Tall Closed Restioland in Sieben *et al*. (2004).
- Plot 8 was related to community 5.2: *Nebelia fragarioides – Staberoha cernua* Closed Short Shrubland in Sieben (2003).
- Plot 11 was related to community 3.3.2: *Berzelia – Metrosideros* Tall Fynbos of the Rocky Streams in Boucher (1978).

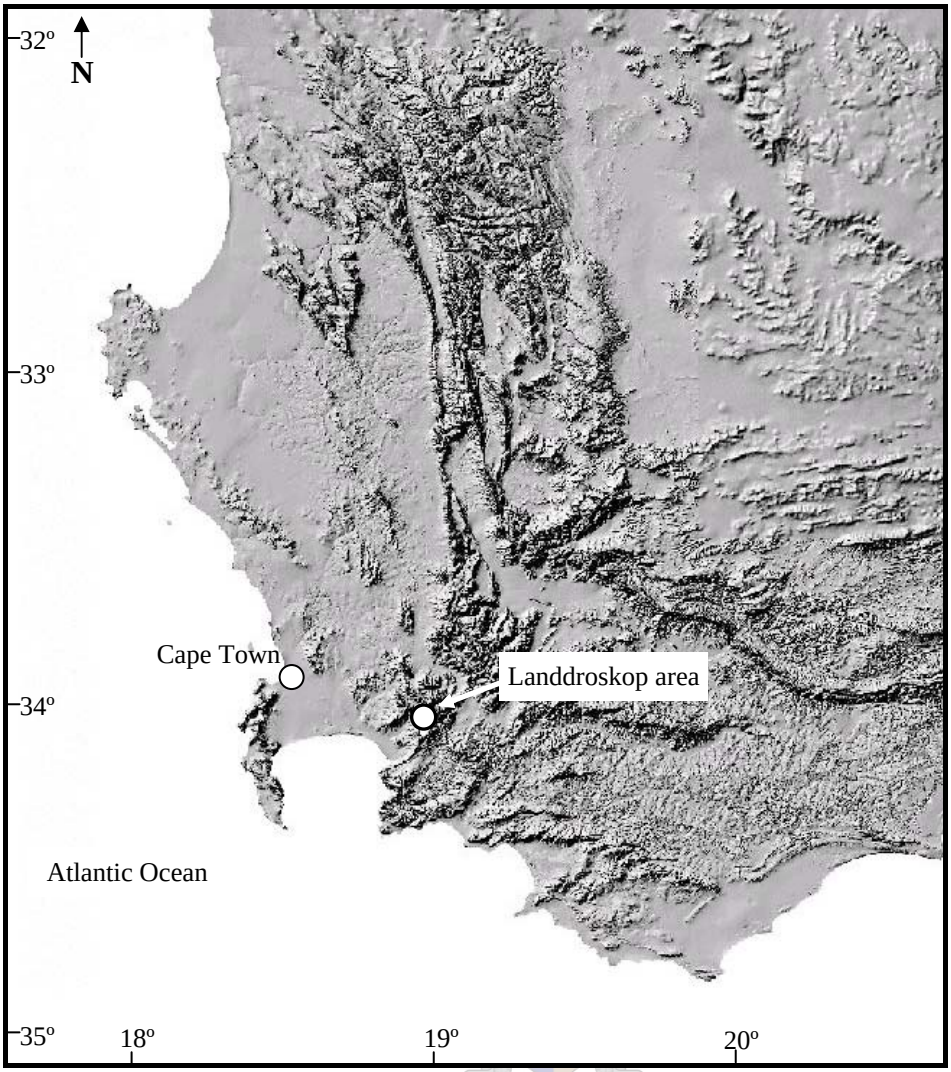

Figure 2.1. Map showing the location of the study area in the Hottentots Holland Mountains.

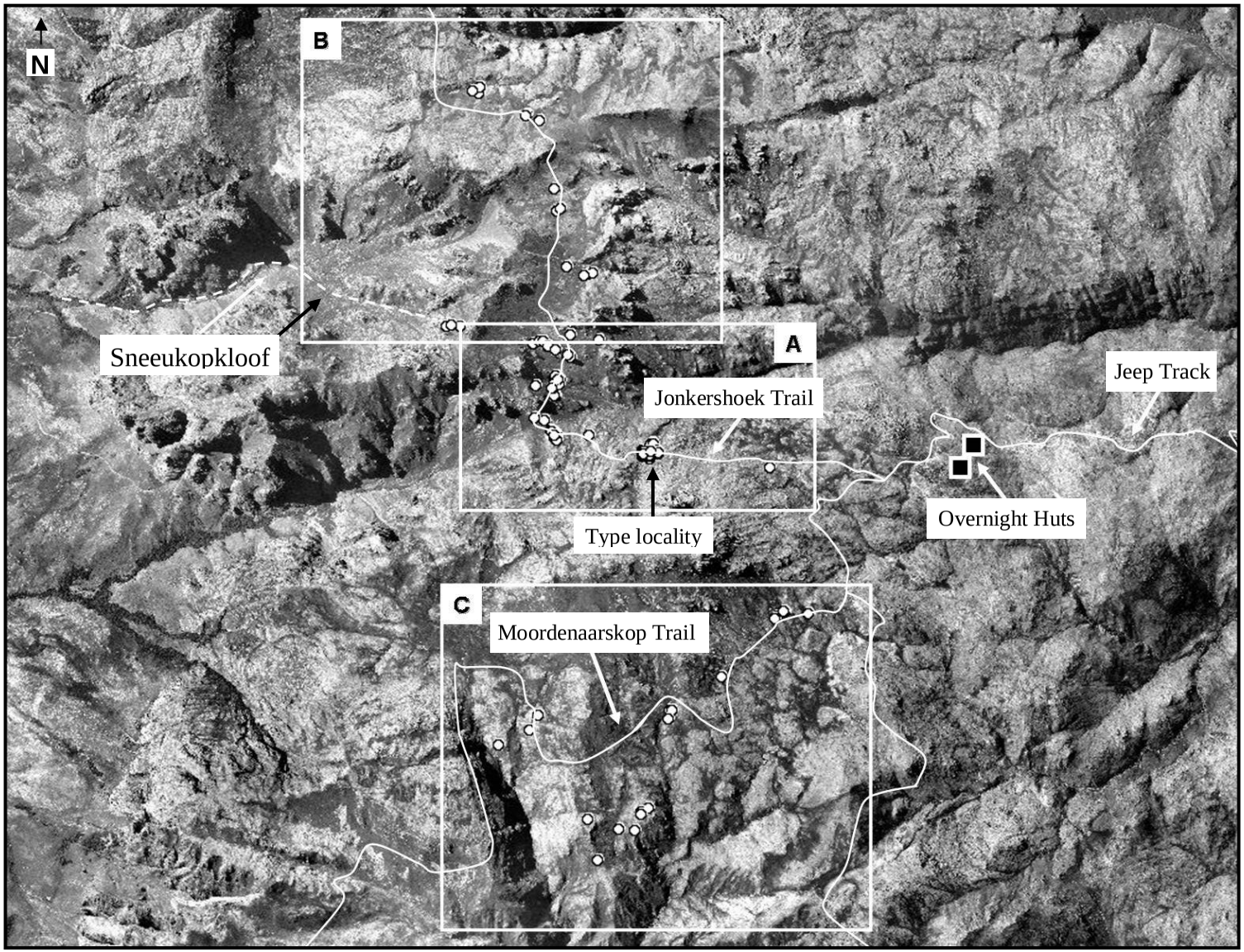

Figure 2.2. The entire survey area in the Hottentots Holland Mountains, with records of *Pseudocordylus nebulosus* individuals indicated by open dots. The dashed line indicates the transect up "Sneeukopkloof". See blocks A-C enlarged in figures 2.3-2.5.

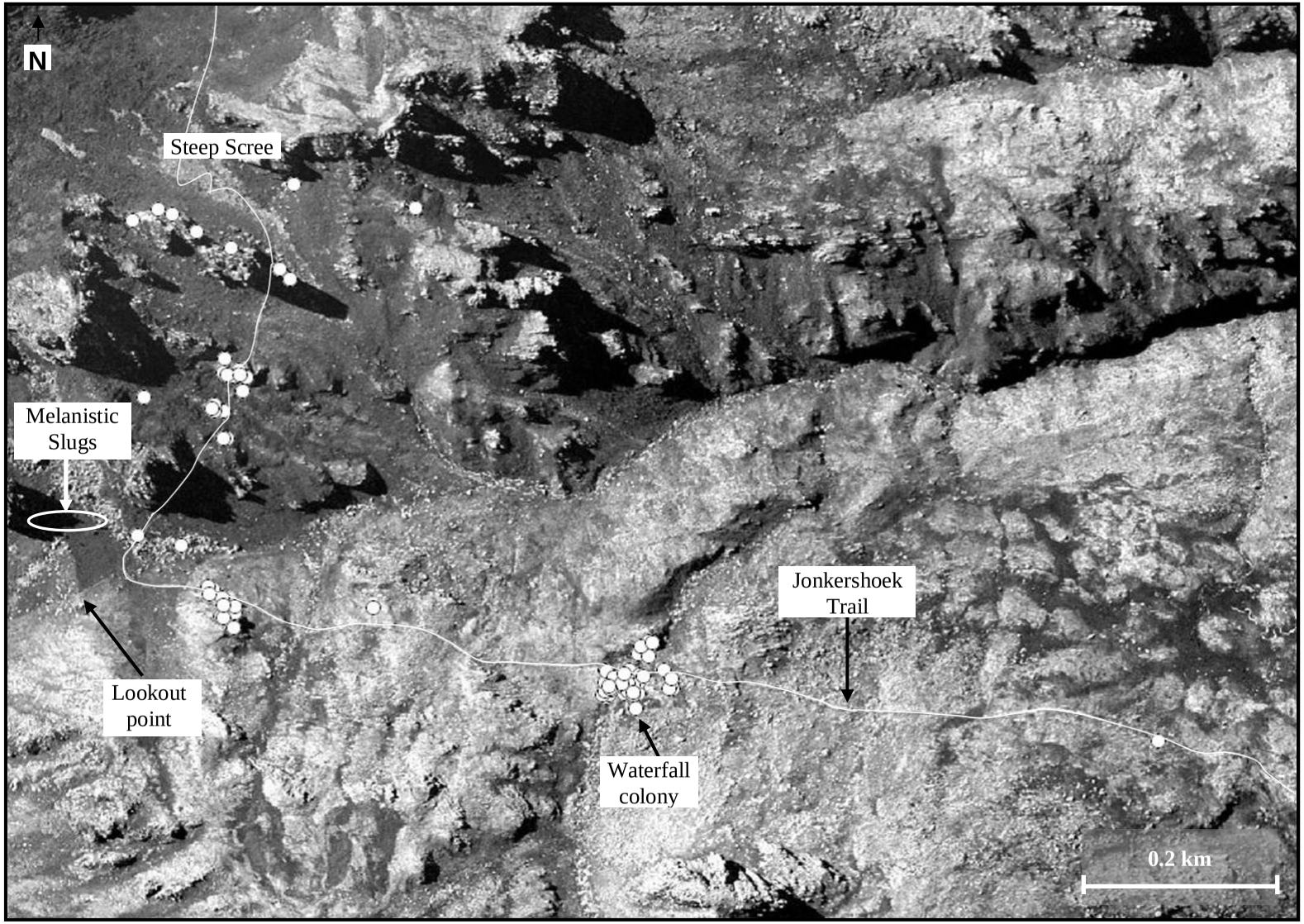

Figure 2.3. Block A enlarged, showing the Waterfall colony and the trail in the direction of the Jonkershoek Valley.

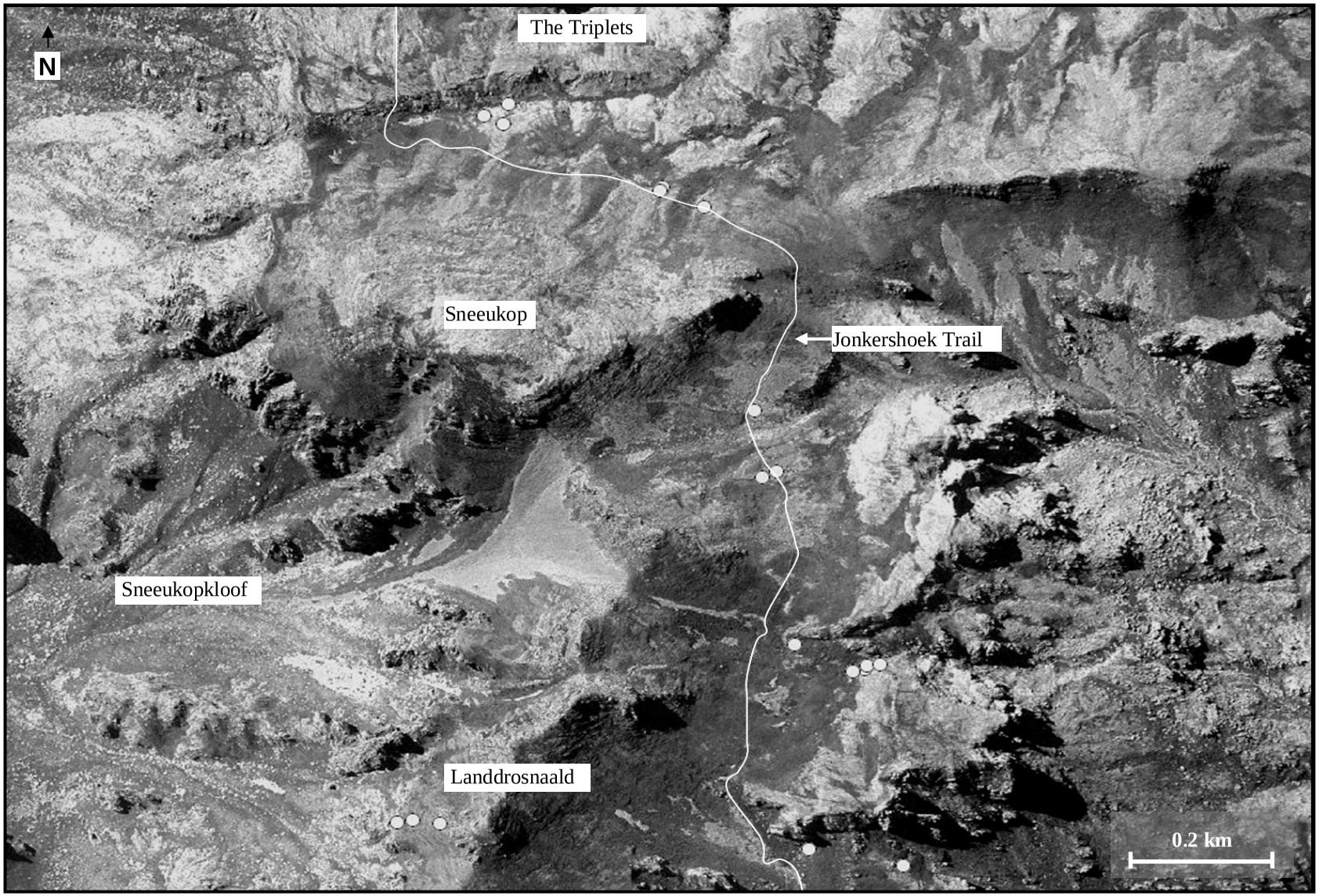

Figure 2.4. Block B enlarged, showing the Jonkershoek Trail and the northernmost boundary before The Triplets.

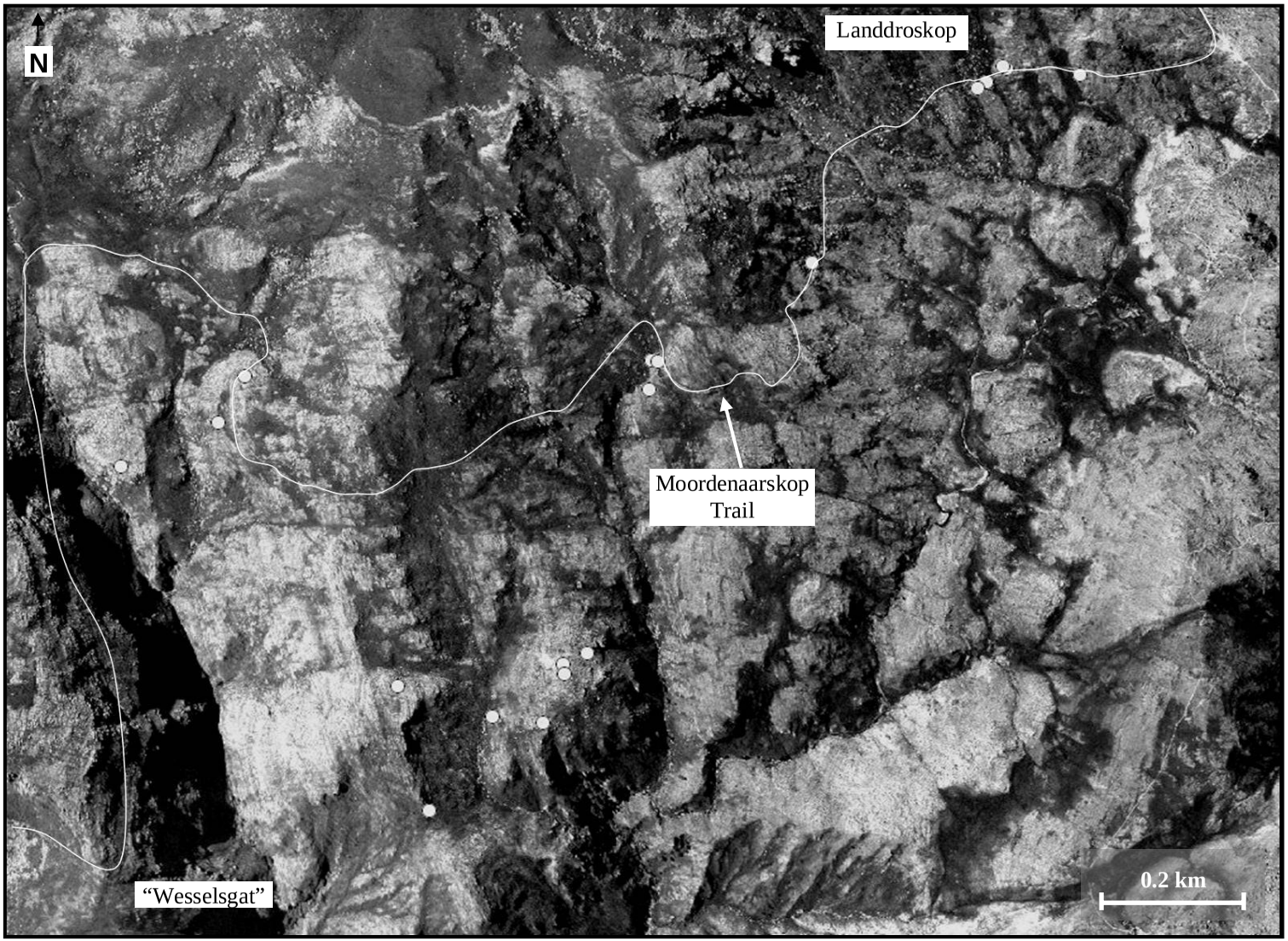

Figure 2.5. Block C enlarged, showing the secondary trail leading to Moordenaarskop and the southernmost point of the survey at "Wesselsgat".

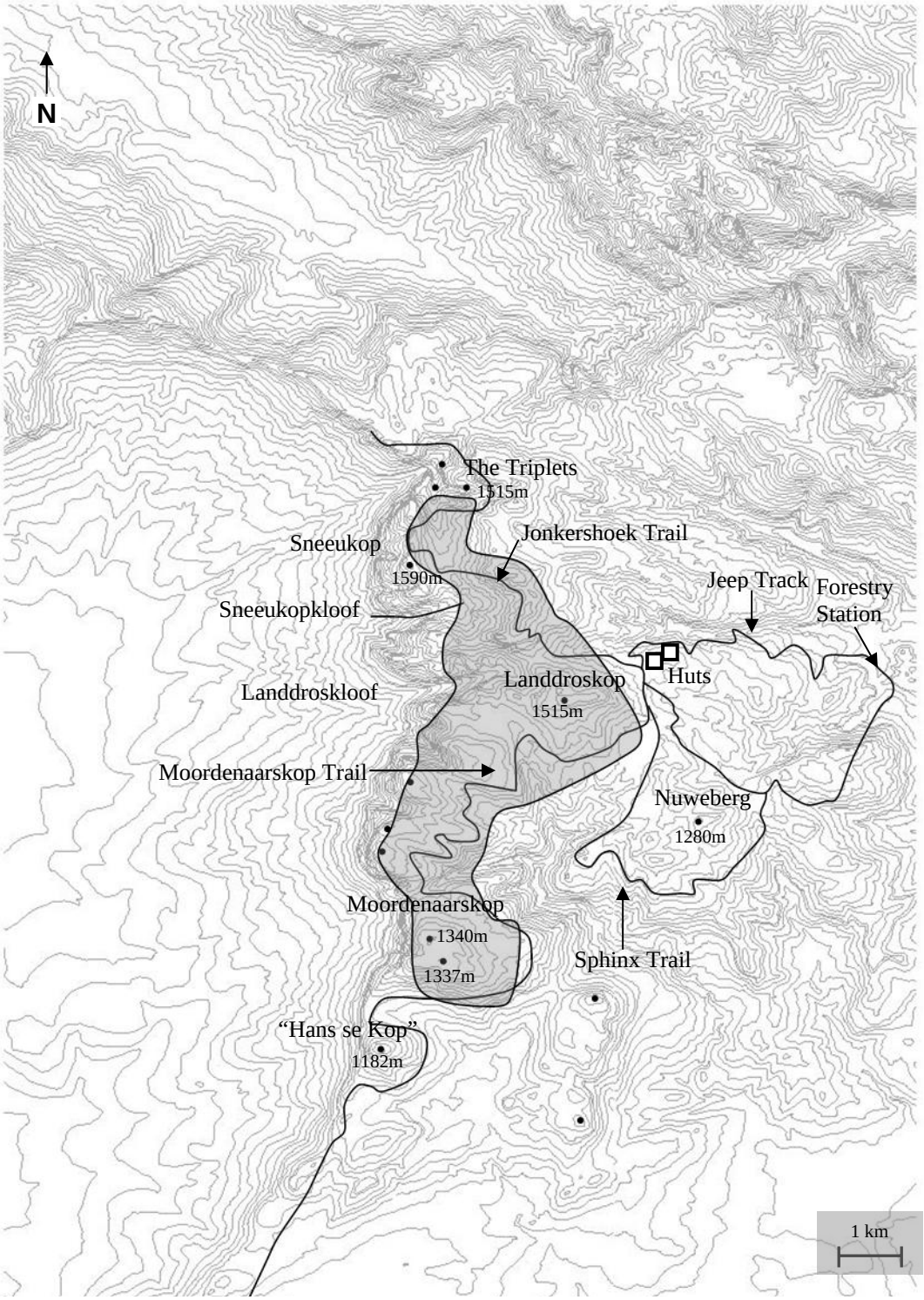

Figure 2.6. Contour map with the shaded area indicating the estimated boundaries of the distribution range for *Pseudocordylus nebulosus*.

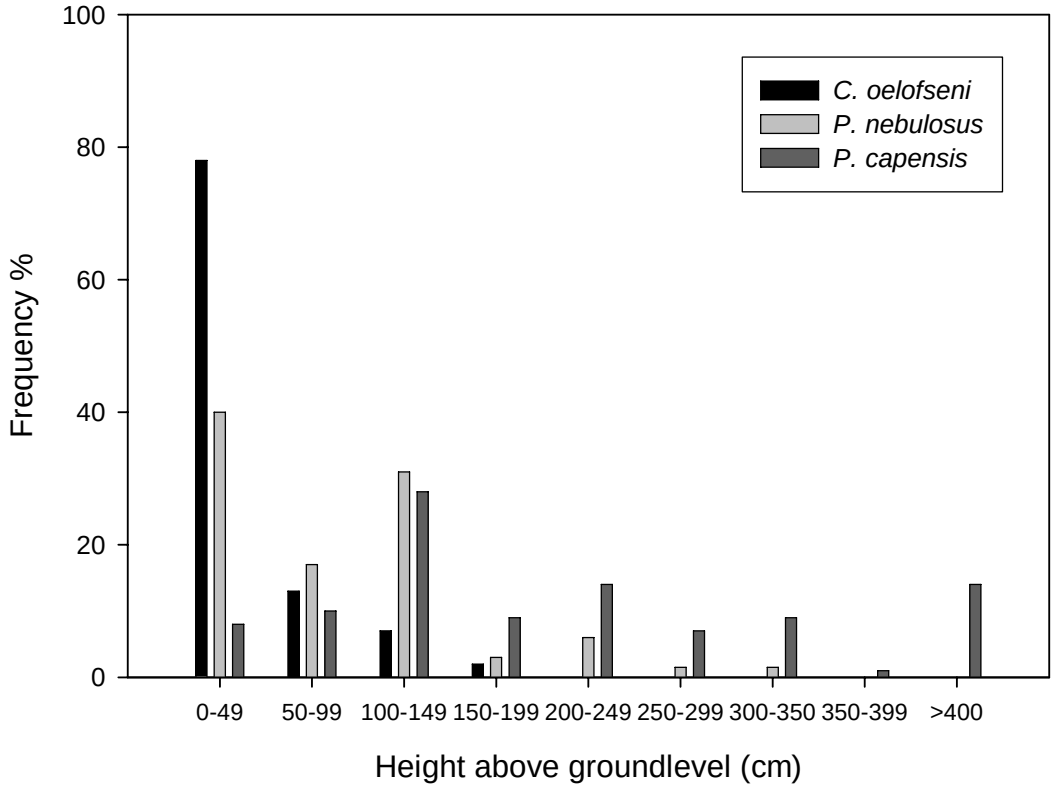

Figure 2.7. Frequency histogram showing the height above ground level at which individuals of each species were recorded.

Table 2.1. Test results for Dunn's Multiple Pairwise Comparison for height above ground level at which individuals of the three species (*C. oelofseni*, *P. capensis* and *P. nebulosus*) were recorded.

Comparison	Diff of Ranks	*Q*	*P*
P. capensis vs *C. oelofseni*	116.232	10.566	< 0.001
P. capensis vs *P. nebulosus*	55.025	4.375	< 0.001
P. nebulosus vs *C. oelofseni*	61.207	5.364	< 0.001

Table 2.2. Number of *Pseudocordylus nebulosus* individuals found in close proximity to water features.

	No. of individuals	% of individuals
Within 10 m of water source	72	53.3
Gully	45	33.3
Scree	11	8.1
Other	7	5.2
Total	135	100

2.4 DISCUSSION

The known range for *P. nebulosus* has been extended considerably, from 0.04 km^2 to an estimated 11 km^2. Within the recorded range, there is no indication of population fragmentation, although, obviously, the availability of suitable rocky habitats will always result in some small-scale fragmentation. It is doubtful that any further populations of *P. nebulosus* will be found in the Hottentots Holland Mountains, or elsewhere in the Cape Fold Mountains. This conclusion is based on the very explicit nature of this species' distribution along the extreme western perimeter of the Hottentots Holland Mountains where the incidence of orographic fog and cloud cover is exceptionally high. Sirgel (1985) reported that the locality is regularly covered in mist, normally accompanied by rain or drizzle, for at least a few hours each day over 200 days of the year, ensuring cool and damp conditions. It is also located in one of the highest rainfall areas in South Africa (Van Wilgen *et al*., 1992; Sieben, 2003). The particular preference for moist areas displayed by this species, underlines its very narrow habitat requirements and it is doubtful that there are any other areas in the Hottentots Holland Mountains or elsewhere where similar conditions prevail.

With an estimated distribution range of only 11 km^2, *P. nebulosus* will always have to be a species of conservation concern. In light of the range extension reported here, and with the knowledge that within a large part of its range, it occurs in highly inaccessible terrain, illegal collecting for the pet trade may not be as serious a threat as was originally feared (Baard *et al*., 1999). Commercial exploitation of the CFR herpetofauna has, however, become a real threat in recent years, especially because of the high number of endemic species in the area (Baard *et al*., 1999) and possible trade in *P. nebulosus* should be monitored continuously. The Landdroskop area is traversed by a series of popular hiking trails and may receive up to 12 000 visitors per year

(Cape Nature, pers. comm.). It should thus be fairly easy for collectors to access the area where *P. nebulosus* occurs, undetected.

Poor fire management is listed as one of the main threats to biodiversity in the CFR (Baard & De Villiers, 2000; Van Wilgen, *et al*., 1992). On average, most fynbos plant communities burn every 12 to 15 years (Cowling & Richardson, 1995). A long interval between fires will lead to a dense overgrowth of vegetation, limiting the number of basking sites available to cordylid lizards of the Cape Fold Mountains, all being heliothermic baskers. Too frequent fires, as well as extremely intense fires, can, however, have a strong negative impact, lowering already small animal and plant populations to a critical threshold of survival from which they will be unable to recover (Baard *et al*., 1999). Being rock-dwelling and showing a preference for moist areas, fire will probably have little direct impact on *P. nebulosus*. The intensity of a fire may, however, be exacerbated by the presence of invasive plant species, some of which give off 300% more heat when burned compared to natural vegetation (Calvin & Wettlaufer, 2000). Alien vegetation may also have other detrimental effects on biodiversity by altering natural habitats (Van Wilgen *et al*., 1992). Within the range of *P. nebulosus*, alien infestation is completely under control and at present poses no threat to this lizard.

Competition for resources and interference competition among closely related species has been documented in a wide range of taxa from most major vertebrate lineages (e.g. birds: Bourski & Forstmeier, 2000; mammals: Tannerfield *et al*., 2002; fishes: Bay *et al*., 2001; amphibians: Brodman & Jaskula, 2002; and reptiles: Langkilde & Shine, 2004). With three melanistic cordylid species, two of which are sister species, co-occurring in the area, the possibility exists that during future periods of environmental stress, brought about by the predicted increase in global

temperatures (Midgley *et al*., 2001; IPCC, 1990, 1996a, 2001a), competition for resources among these three species may increase and that *P. nebulosus*, having the strictest habitat requirements of the three, may be affected the most. Our data, however, show that, although the range of *P. nebulosus* completely overlaps with those of *P. capensis* and *C. oelofseni*, the observed habitat partitioning with regard to crevice selection, will prevent any significant competition among the three species during periods of environmental stress. Cordylid lizards are sit-and-wait foragers that spend the largest part of their general maintenance behaviour in close proximity to their shelter crevices (Cooper *et al*., 1997). The specific sites where lizards were recorded, be it basking or sheltering inside crevices, can thus be taken as representative of their shelter-site choice and the height above ground level recorded, as an accurate descriptive measurement to distinguish between microhabitats. The interspecific difference in microhabitat use we encountered is probably linked to body size, as has been recorded in other lizard assemblages (e.g., Langkilde & Shine, 2004).

The projected rise in global temperatures, predicted to be quite severe over the next 50–100 years (Midgley *et al*., 2001; IPCC, 1990, 1996a, 2001a), is probably the most serious threat facing *P. nebulosus.* It is predicted that, as the climate changes, the character of extreme weather events, such as cold snaps and droughts, will also change (Karl *et al.*, 1995), necessitating relatively rapid habitat changes for most animals (Parmesan *et al*., 2000). Rapid movements by birds are possible because they can fly, but for reptiles such movements are much more difficult. Species such as *P. nebulosus*, already restricted to montane habitat islands at the highest elevations, have nowhere to move to and consequently may face extinction. Climatic changes are likely to be most important for taxa in montane areas, where even a small rise in mean

temperature may enable lowland animals and plants to penetrate much further up the mountains (e.g. Hughes, Cawsey & Westoby, 1996a, b; Gibbons *et al.*, 2000). This may lead to changes in species composition at higher altitudes, with species characteristic of lower slopes co-occurring with high altitude species and placing further pressure on the limited resources (Pounds *et al*., 1999). At the Landdroskop area, rupicolous lizard species occurring on the lower slopes below 1 200 m include *Pseudocordylus microlepidotus* and *Agama atra atra*. Due to climate change these two species may move to higher elevations and compete for resources with the other melanistic cordylids present there. In the case of *P. microlepidotus*, individuals have large home ranges and occur at low densities (Mouton *et al*., 2005), it is thus unlikely that significant competition for resources should occur if they were to overlap in distribution with *P. nebulosus*. As *A. a atra* falls into a different family they may have totally different habitat requirements than cordylid lizards and competition for resources would be unlikely.

Currently, all climate models predict an increase in global mean precipitation (Hughes, 2000). This is however not the case for parts of the Western Cape, which, according to the predictions of Midgley *et al*. (2001), may lose a significant portion of its current winter rainfall. It is not yet clear what the exact effects of climate change will be on the CFR and the unique mistbelt area in the Hottentots Holland Mountains, but because of the already small range of *P. nebulosus* and the constraints of a melanistic body colour in warm climates, it may be one of the first animal species in the Hottentots Holland Mountains to show signs of stress. It may thus be a key indicator species of environmental change in the area.

There is at least some indication that *P. nebulosus* has an affinity for moist areas, but more detailed analyses are needed for confirmation of this. Melanistic

forms have been found to be at an advantage under conditions of low temperature and a limited radiative regime, because a dark ectotherm will heat up faster and reach a higher equilibrium temperature (Lusis, 1961; De Jong *et al*., 1996). This could be advantageous for *P. nebulosus* in the Landdroskop area where the mistbelt, which occupies the upper limits for most days of the year, causes conditions of limited solar radiation (Sirgel, 1985). On the other hand, its melanistic body colour could also make it more susceptible to heat stress, possibly explaining why *P. nebulosus* individuals would congregate around water sources and seepage areas. On several occasions during the survey, lizards were even observed to position themselves under the spray of small waterfalls and in shallow pools. Global warming may thus already be impacting on these lizards, restricting them to cool moist areas. As some plant species or species assemblages can be associated with moist conditions, where open water is not visible, the presence of these species can be used as indicators of wet areas. If *P. nebulosus* is indeed linked to water sources, this could be used to pinpoint other sites in the distribution area where they are likely to occur. Although our data showed that *P. nebulosus* has an affinity for water sources, a further in-depth study is needed to corroborate this before any definite conclusions can be made.

Baard *et al*. (1999) proposed that *P. nebulosus* be placed in the *Vulnerable* category of the IUCN's Red Data list, because of its restricted distribution and the threat of commercial exploitation. With the new available distribution data it is recommended that this status is maintained. Although its distribution range is considerably smaller than the 100 km^2 specified by the IUCN's *Critically Endangered* criteria, information on the rate of decline in area of occupancy as well as evidence of decline in numbers is also required before a species can be given this status (IUCN, 2001). This information is currently not available for *P. nebulosus* and will only

become available after a longterm monitoring programme has been initiated. This study provides baseline data that could be used to monitor and predict declines and fluctuations in the future. As it would not be possible to survey the entire distribution range in a monitoring programme it is recommended that sites where concentrations of lizards were recorded be monitored as representative of the total population.

CHAPTER 3

SEXUAL DIMORPHISM IN MONTANE CORDYLID LIZARDS: A CASE STUDY OF THE DWARF CRAG LIZARD, *PSEUDOCORDYLUS NEBULOSUS*

3.1 INTRODUCTION

In lizards, the degree and direction of sexual dimorphism can provide substantial information about many aspects of the general biology of a species. For example, when males are considerably larger than females and also have larger heads, it can be indicative of a polygynous mating system (Stamps, 1983; Mouton & Van Wyk, 1993). Where females are the larger sex, more often than not, it is indicative of a harsh environment and environmental pressure on females to produce either larger or more offspring (Van Wyk & Mouton, 1998; Du Toit *et al*., 2003). Where sexual dimorphism has a genetic basis, it can be the result of either sexual selection or natural selection or both (Koenig & Albano, 1986). Sexual dimorphism can, however, also result from a variety of local environmental processes (Gibbons & Lovich, 1990; Shine, 1990). Adult growth and survival rates, for example, may vary from locality to locality, resulting in varying sexual differences in mean body size (Stamps, 1983).

Information on sexual dimorphism and mating systems is available for a number of cordylid species. Members of the genus *Platysaurus* (15 species) are highly sexually dimorphic in colour pattern (Broadley, 1978; Branch, 1998), but no information on sexual size dimorphism is available. Information on sexual size dimorphism is available for five of the 32 *Cordylus* species. Two of the five are terrestrial and three are rock-dwelling. In both the terrestrial species, females are the

larger sex, but males have larger heads than females (Van Wyk, 1992; Mouton *et al*., 2000). In the three rock-dwelling species, males are larger than females and also have larger heads (Cordes *et al*., 1995; Mouton *et al*., 1999). Information on sexual size dimorphism is available for only one of the three arboreal snake-like *Chamaesaura* species. In the Cape Grass Lizard, *Chamaesaura anguina*, females attain considerably larger body sizes than males and there is a distinct correlation between body size and clutch size (Du Toit *et al*., 2003).

Members of the genus *Pseudocordylus* (six species) are all montane species, occurring in the Cape Fold and escarpment mountain ranges of South Africa. Frost *et al*. (2001) found that *Pseudocordylus* consists of two separate clades that do not form a monophyletic group. The Drakensberg Crag Lizard, *P. melanotus subviridis*, displays pronounced male-biased sexual dimorphism in size and coloration and also has a polygynous mating system (Mouton & Van Wyk, 1993; Griffith, unpublished data). In the closely related Cape Crag Lizard, *P. microlepidotus*, however, there are no noteworthy sexual differences in body size, but males have larger heads than females (Sachse *et al*., 1997; Mouton *et al*., 2005). In the Graceful Crag Lizard, *P. capensis*, on the other hand, females reach larger body sizes than males, but no noteworthy sexual differences in head size occur (Van Wyk & Mouton, 1998). Given the energy constraints experienced at high altitudes, one would have expected less variation in degree and direction of sexual size dimorphism among montane cordylids. It is clear that information about more montane species is needed to understand the observed variation.

The aim of this study is to provide information about sexual dimorphism in an additional montane cordylid and to discuss the observed variation in sexual size dimorphism among montane cordylids. Sexual size dimorphism information is

provided for the Dwarf Crag Lizard, *Pseudocordylus nebulosus*, a melanistic species occurring at an altitude of 1 200 m within the mistbelt of the Hottentots Holland Mountains in the Western Cape Province, South Africa (Mouton & Van Wyk, 1995; see Chapter 2). This species was only discovered in 1995 (Mouton & Van Wyk, 1995) and, having a restricted range of only 11 km^2, is considered to be a species of conservation concern (Baard *et al*., 1999; see Chapter 2).

3.2 MATERIALS AND METHODS

3.2.1 Study Area

Data on *Pseudocordylus nebulosus* were collected in the Hottentots Holland Mountains, the only known locality where this species occurs. At an altitude of 1 000-1 500 m, the area where *P. nebulosus* occurs lies within the mistbelt of the mountains and receives orographic fog or cloud cover for more than 200 days per year (Sirgel, 1985). The area mainly receives winter rain with the mean annual rainfall in the general area being of the highest in South Africa, exceeding 1 200 mm (Dent *et al*., 1989). The vegetation is typical Sandstone Fynbos (Mucina & Rutherford, 2004). An area of approximately 5 km^2 was intensively surveyed for *P. nebulosus* between November 2003 and September 2004.

3.2.2 Morphological Measurements

Data were recorded for all *P. nebulosus* individuals captured in the field, irrespective of size and sex. Adult males were identified by the presence of hemipenal bulges and patches of generation glands on the ventral aspect of the thighs. Females of this species do not possess generation glands (Mouton & Van Wyk, 1995). Size at sexual maturity was taken as the size at which generation glands start to

differentiate in young males. In *P. capensis*, the sister species of *P. nebulosus*, the size at which generation glands were found to differentiate was narrowly correlated with the size at sexual maturity (Du Toit, 2004). All reports on size at sexual maturity in cordylids, except for *Cordylus macropholis* (Mouton *et al*., 2000), suggest that the size at maturity is the same for both sexes (Van Wyk, 1989; 1991; 1992; Flemming & Van Wyk, 1992; Flemming, 1993a,b,c; Mouton & Van Wyk, 1993; Van Wyk & Mouton, 1996). We therefore made the assumption that both male and female individuals larger than the size at which generation glands first start to develop in males, can be classified as adults. For *P. nebulosus* this size was determined at 60 mm snout-vent length (SVL). It was also at this size that femoral glands became active, secreting plugs of a waxy material (Van Wyk & Mouton, 1992; Mouton *et al*., 1998). Thus, individuals with active femoral glands, lacking generation glands, were classified as adult females.

For each individual the following measurements were taken to the nearest 0.01 mm using digital callipers: snout-vent-length (SVL), head length (HL, the distance between the tip of the snout to the anterior edge of the tympanic opening), head width (HW), head depth (HD) and tail length (TL). Generation and femoral glands were counted in the field using a handheld magnifying glass (10x). Individuals were also examined for the presence of scars, including missing digits or part thereof, part of the tail missing, regenerated tails or any other visible injuries on the body.

3.2.3 Data Analysis

In cases where data sets were abnormally distributed, the Mann-Whitney U-test was used to compare two groups. Scaling of variables with increasing body size was determined using least square regression analysis of log-transformed variables

versus log SVL. Analysis of covariance (ANCOVA), with sex as factor and SVL as covariate, was used to compare the slopes of the regressions for head and tail measurements of adult males, adult females and juveniles.

Sexual size dimorphism (SSD) for the sample was quantified by a simple size dimorphism index (SDI):

$$\frac{\text{mean SVL of adults of larger sex}}{\text{mean SVL of adults of smaller sex}}$$

with the result being defined as positive when females are larger and negative when males are larger (Gibbons & Lovich, 1990). In addition, a maximum size dimorphism index (SDI_{max}), based on the mean SVL of the largest 20 % of each sex, was calculated. A size dimorphism ratio was also calculated as the mean female trait (SVL, HW, HL, HD, TL) over the mean male trait. The percentage dimorphism was then taken as the absolute value of [(dimorphism ratio – 1) x 100] (Cordes *et al*., 1995).

A Pearson Correlation was used to test for relationships between body size and the number of epidermal glands for males and females. A *Z*-test was conducted to test for sexual differences in scar frequency. Probability values (*P*) smaller than 0.05 were considered significant throughout the analysis. Data analysis was done using the computer programmes Statistica™ and SigmaStat™ for Windows.

3.3 RESULTS

3.3.1 Sex ratio

Data were obtained for 87 lizards, including 26 adult males, 49 adult females, and 12 indeterminates. The recorded adult sex ratio was 1:1.88 in favour of females.

3.3.2 Epidermal glands

Generation glands were found to be present in males only. The number ranged from 6 – 38 (Fig. 3.1a) and was significantly correlated with body size (Pearson Correlation Coefficient = 0.632, $P < 0.001$). Both adult males and adult females possessed active femoral glands. The number ranged from 14 – 21 in males and from 13 – 21 in females (Fig.3.1b). Males had significantly more active femoral glands than females (Mann-Whitney Rank Sum Test: $T = 1288.5$, $P < 0.001$). The number of femoral glands was significantly correlated with body size for males (Pearson Correlation Coefficient = 0.509, $P < 0.05$) and females (Pearson Correlation Coefficient = 0.432, $P < 0.05$).

3.3.3 Sexual Size Dimorphism

From the body size class distributions, it appears that females reach slightly larger body sizes than males (Fig. 3.2). Males ($N = 26$) ranged from 60.29 mm to 76.60 mm, while females ($N = 49$) ranged from 60.22 mm to 80.68 mm. The mean SVL of females (71.51 mm ± 4.77 SD) was significantly larger than the mean SVL of males (69.84 mm ± 4.11 SD; Mann-Whitney Rank Sum Test: $T = 809.5$, $P = 0.048$). A significant difference was also recorded between the mean SVL's of the largest 20% of each sex. The mean SVL for the largest 20% of females ($N = 10$) was 76.83 mm ± 1.703 SD and the mean SVL for the largest 20% of males ($N = 5$) was 74.47 mm ± 1.206 SD (Mann-Whitney Rank Sum Test: $T = 22.000$; $P = 0.032$). The SDI for the sample was calculated as 1.03 and the SDImax as 1.413.

Statistics of the regression for head width, head length, head depth and tail length versus SVL are given in Table 3.1 and the regression plots in Figures 3.3a-c. An ANCOVA indicated that the increase in head length with increasing SVL was

significantly larger in juveniles than in adult males and females, and significantly larger in adult males than in adult females (Table 3.2; Fig. 3.3a). The increase in head width with increasing SVL was significantly larger in adult males than adult females and juveniles (Table 3.2; Fig. 3.3b). Although the increase in head depth with increasing SVL was significantly larger in males than females, the difference between adult males and juveniles and adult females and juveniles was not significant (Table 3.2; Fig. 3.3c).

The larger male head width measurements suggested a percentage male-biased dimorphism of 4.8%. This was also the case for head length and head depth with a percentage male-biased dimorphism of 3.6% and 4.7%, respectively. There was, however, a percentage female-biased dimorphism of 2.4% regarding SVL.

The increase in tail length with increasing SVL did not differ significantly between the three size and sex classes. Although there was a significant correlation between the increase in tail length with increasing SVL in adult females and juveniles, this was not the case for adult males (Table 3.2; Fig. 3.4). No obvious sexual differences were noted in adult coloration, with both sexes being melanistic and having characteristic yellow blotches on the dorsal surface.

3.3.4 Scar Frequency

Of the male sample (N = 26), 31% displayed scars, while 18% of the female sample (N = 49) displayed scars. There was no significant difference in scar frequency between the male and female samples (Z-test: Z = 0.931; P = 0.352).

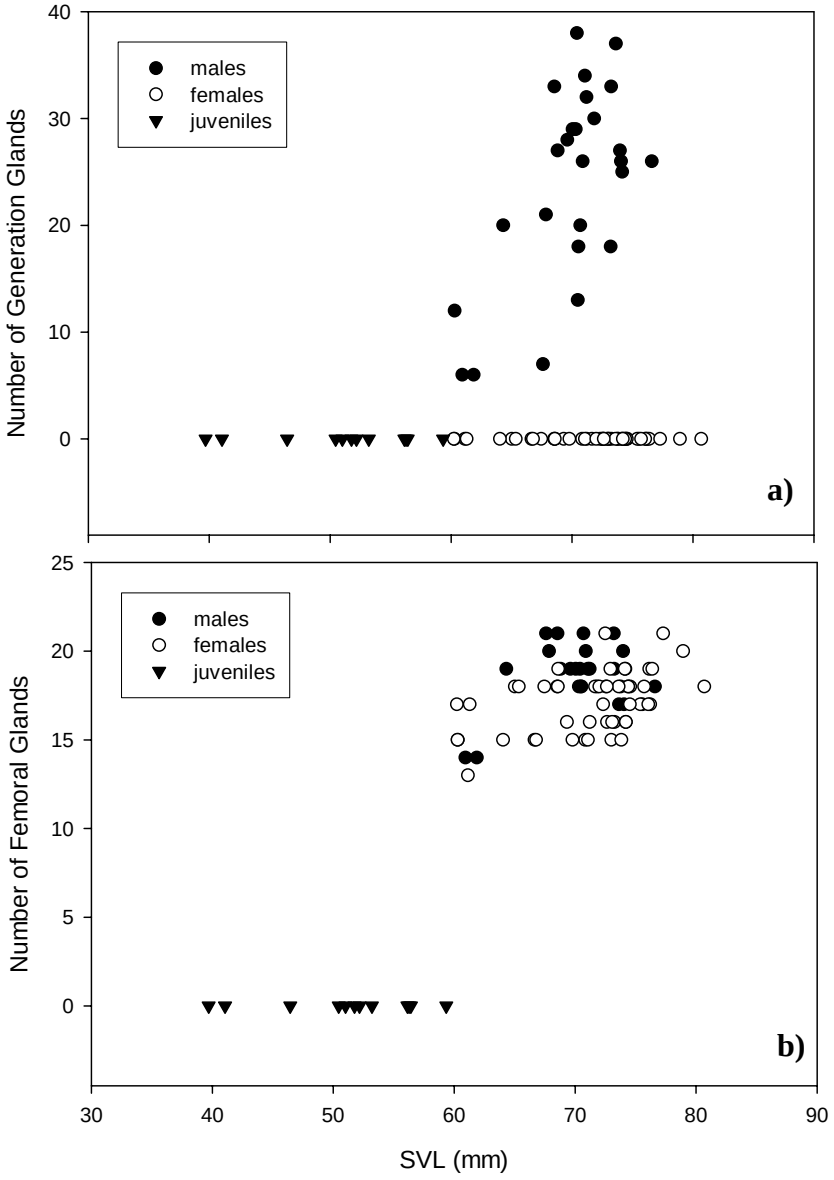

Figure 3.1. Scatterplot of a) the number of generation glands and b) the number of femoral glands, versus snout-vent length in *Pseudocordylus nebulosus*.

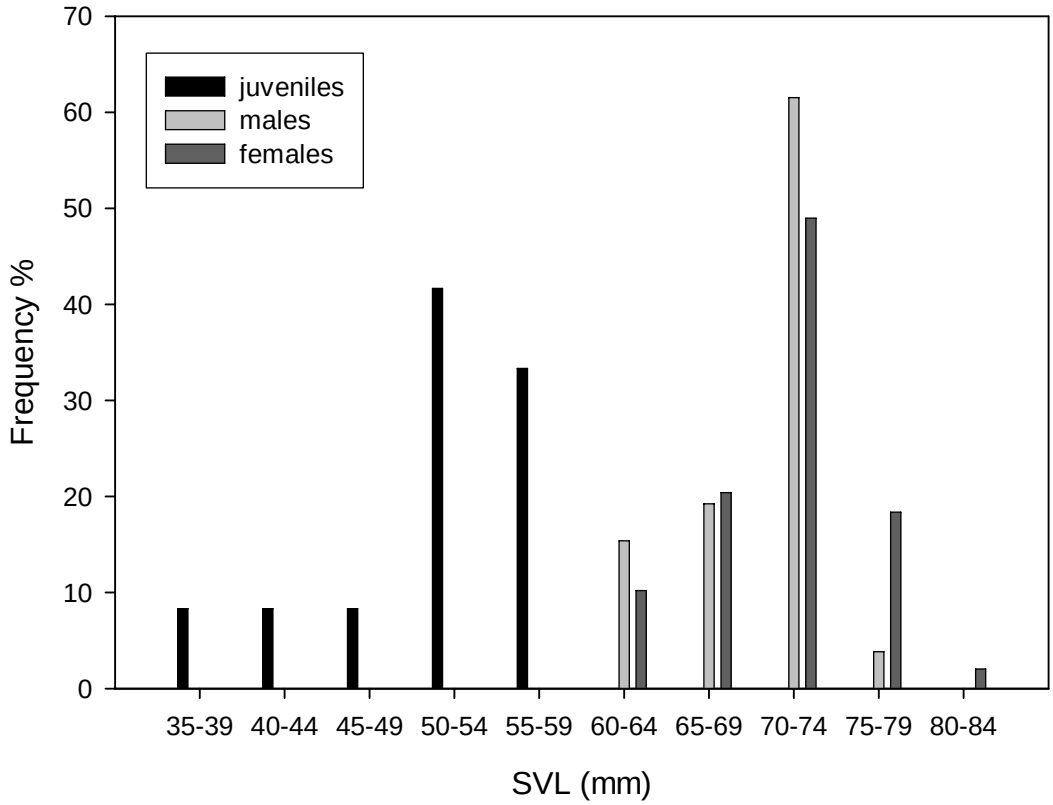

Figure 3.2. Frequency histogram of body size distribution for *Pseudocordylus nebulosus* individuals.

Table. 3.1. Regression statistics for comparisons of relationships between head and tail measurements and body size (SVL) for males, females and juveniles of *Pseudocordylus nebulosus*. Head length (HL), head width (HW), head depth (HD), tail length (TL)

Measurement	R2	F	d.f.	*P*	Slope	Intercept
logHL/logSVL						
Males	0.701	57.664	1	< 0.001	0.725	-0.019
Females	0.690	104.485	1	< 0.001	0.504	0.369
Juveniles	0.968	298.03	1	< 0.001	0.833	-0.238
logHW/logSVL						
Males	0.714	60.025	1	< 0.001	1.023	-0.713
Females	0.481	43.58	1	< 0.001	0.549	0.134
Juveniles	0.883	75.546	1	< 0.001	0.977	-0.66
logHD/logSVL						
Males	0.669	48.5	1	< 0.001	1.202	-1.281
Females	0.486	44.481	1	< 0.001	0.830	-0.625
Juveniles	0.807	41.753	1	< 0.001	0.842	-0.667
logTL/logSVL						
Males	0.056	1.133	1	> 0.05	0.316	1.383
Females	0.237	11.467	1	< 0.05	0.764	0.554
Juveniles	0.604	13.74	1	< 0.05	0.779	0.518

Table 3.2. ANCOVA results for comparison of regression coefficients of head length, head width, head depth and tail length versus SVL among sexes and age classes of *Pseudocordylus nebulosus*

	Comparison of Slopes		
	F	d.f.	*P*
Head length			
M vs F	57.617	1	< 0.001
M vs J	9.742	1	< 0.05
F vs J	14.122	1	< 0.001
Head width			
M vs F	38.514	1	< 0.001
M vs J	4.222	1	< 0.05
F vs J	9.918	1	< 0.05
Head depth			
M vs F	23.724	1	< 0.001
M vs J	2.448	1	> 0.05
F vs J	1.464	1	> 0.05
Tail length			
M vs F	0.026	1	> 0.05
M vs J	1.785	1	> 0.05
F vs J	0.217	1	> 0.05

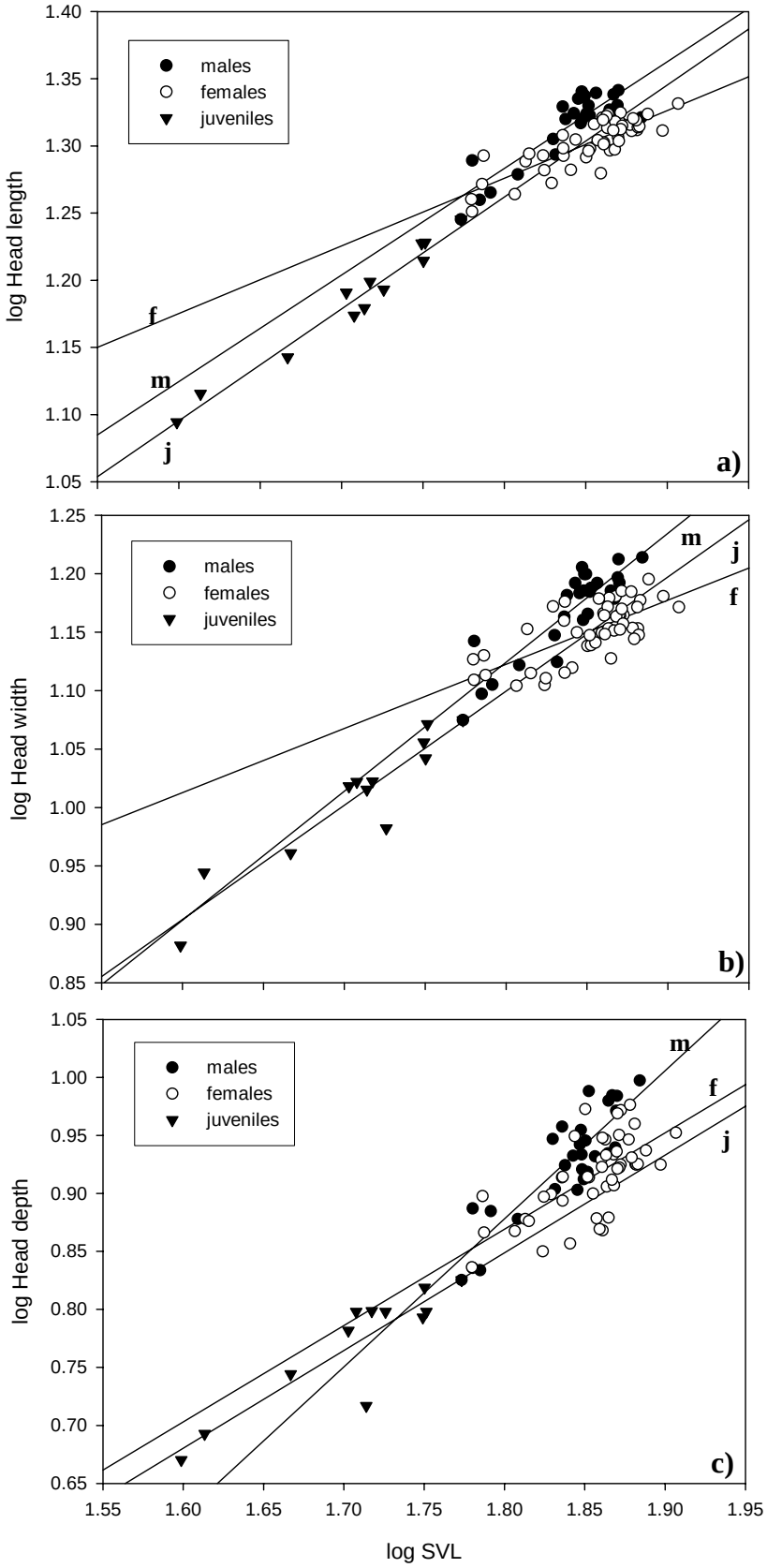

Figure 3.3. Regression plots for a) head length, b) head width and c) head depth versus SVL for *Pseudocordylus nebulosus*.

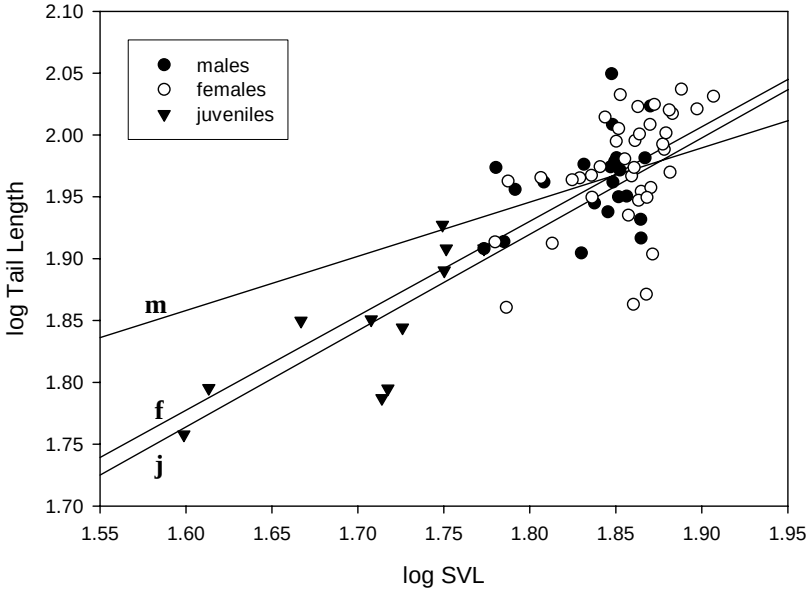

Figure 3.4. Regression plot for tail length versus SVL for *Pseudocordylus nebulosus*.

3.4 DISCUSSION

In this study, a highly female-biased adult sex ratio was recorded for *Pseudocordylus nebulosus*, females were found to reach larger body sizes than males, and males were found to have relatively larger heads than females. Although highly female-biased adult sex ratios have been recorded for other cordylid species, e.g., *Cordylus macropholis* (Mouton *et al*., 2000; Nieuwoudt *et al*., 2003), the recorded female bias in *P. nebulosus* may be the result of sampling error. In the field, *P. nebulosus* was mostly located by searching for basking individuals. It is a general trend among heliothermic lizards that in cold environments, gravid females make use of behavioural thermoregulation more than males (Shine *et al*., 2003) and the possibility thus exists that more females of *P. nebulosus* were collected because they were easier to locate than males. Sampling during December, which is a warm month, was clearly female-biased with 25 out of the 31 adult individuals sampled being female (1:4 in favour of females), while the sex ratio was close to 1:1 for the other sampling months (April – May, August and November).

Female-biased dimorphism in body size reported here for *P. nebulosus*, has also been recorded for its sister species, *P. capensis* (Van Wyk & Mouton, 1998). These authors concluded that the female-biased sexual size dimorphism observed in *P. capensis* reflects fecundity selection in that offspring need to be large at birth in order to survive in a predictable unfavourable environment at high altitudes. In their study of *P. microlepidotus*, co-occurring with *P. capensis* and *P. nebulosus* in the Cape Fold Mountains, Mouton *et al.* (2005), however, concluded that the absence of notable sexual dimorphism in body size in this species, is due to the net effect of sexual selection for larger body size in males due to territoriality, and fecundity selection for larger body size in females to produce more offspring in an unpredictable

environment. Adults have large home ranges and neonates will have to disperse relatively long distances to find suitable microhabitats and will thus face many dangers (Mouton *et al*., 2005). For these two species then, two contrasting explanations have been advanced to explain female-biased sexual size dimorphism, or lack thereof, namely fecundity selection for larger offspring size, increasing survival in a predictable adverse environment, and, secondly, fecundity selection to produce more offspring, increasing survival in an unpredictable adverse environment.

Being associated with conditions of limited solar radiation, *P. nebulosus* and *P. capensis* are cool-adapted species (Badenhorst, 1990), occurring at high altitudes, but *P. microlepidotus* is also found at high altitudes in the Cape Fold Mountains (Branch, 1998). Why would the three species have different life history strategies in the same geographical area? To complicate matters even further, *P. melanotus subviridis*, occurring in the eastern escarpment mountains at altitudes as high as 3 000m, shows pronounced male-biased dimorphism (Mouton & Van Wyk, 1993).

To interpret the observed variation in sexual size dimorphism among montane cordylids correctly, it is necessary to evaluate the variation within a phylogenetic context. The genus *Pseudocordylus*, as presently construed, is non-monophyletic and consists of two unrelated clades, the *melanotus-microlepidotus-spinosus-langi* clade on the one hand and the *capensis-nebulosus* clade on the other hand (Frost *et al*., 2001; Melville *et al.*, 2005). It will probably not be meaningful at this stage to compare degree and direction of sexual size dimorphism across these two clades, but it may be informative to make comparisons within clades. *Pseudocordylus microlepidotus* is the sole representative of its clade occurring in the western winter rainfall area, all other species in the clade occurring in summer rainfall areas. In both *P. microlepidotus* (Sachse, unpublished data) and *P. melanotus* (Flemming, 1993b)

the young are born in late summer, i.e., end January, beginning February. In the winter rainfall area, this is the dry period and food availability is expected to be low. The two to three months before the onset of winter will probably not allow for significant growth in neonates before the onset of winter. In the summer rainfall area, the two to three month period before winter should be an important growing period for neonates and should help them to attain body sizes that will see them through the winter. One would predict that, all other things being equal, neonates will be smaller at birth in the summer rainfall areas than in the winter rainfall area and that females in the summer rainfall areas will be relatively smaller than females in the winter rainfall area, in other words that male-biased dimorphism will be more common in summer rainfall areas and female-biased dimorphism in winter rainfall areas. Unfortunately, there are not enough data available on offspring size at birth and growth rates immediately after birth to evaluate this prediction. Reported clutch sizes for *P. microlepidotus* and *P. melanotus* are the same (Sachse, unpublished data, Flemming, 1993b; Branch, 1998), so clutch size is probably a conservative trait not under strict environmental control.

While there is no clear indication that natural selection is at least partly responsible for the observed differences in SSD in *P. microlepidotus* and *P. melanotus*, there is substantial evidence that sexual selection may be largely responsible for the observed differences. There is a distinct difference in social structure between *P. melanotus subviridis* and *P. microlepidotus* (Mouton & Van Wyk, 1993; Mouton *et al*., 2005; Griffiths, unpublished data) and, knowing that sexual selection is probably the most common cause of sexual size dimorphism (Stamps, 1983), one cannot but conclude that the observed differences in sexual

dimorphism between these two species is largely the result of differences in social structure.

In the case of the *nebulosus-capensis* clade, interpretation of the observed female-biased sexual size dimorphism is more difficult. Because the two species are sister species (Frost *et al*., 2001), co-occur in the same area, and show the same degree and direction of sexual size dimorphism, comparison with the sister species of the clade, *Cordylus coeruleopunctatus* (Frost *et al*., 2001), will be required. This species occurs in the southern Cape Fold Mountains where rainfall is aseasonal (Schulze, 1997). Unfortunately, no information is available for *C. coeruleopunctatus*. Comparison with other *Cordylus* species, except the two species that also show female-biased dimorphism, would probably be meaningless in the absence of a complete data set. Female-biased dimorphism has been observed in two terrestrial *Cordylus* species, *C. macropholis* (Mouton *et al*., 2000) and *C. giganteus* (Van Wyk, 1992). In the case of *C. macropholis*, Mouton *et al*. (2000) ascribed the observed dimorphism to the fact that these lizards shelter among stems of *Euphorbia* plants and that a tubular body and shorter legs are required to do this effectively. Diametric reduction will negatively impact on body space available to hold embryos, and to maintain reproductive output, selection apparently favours a longer trunk in females. It is also true that in the terrestrial environment, visibility to conspecifics will not be the same as for rock-dwelling species and that sexual selection pressures will be less (Mouton *et al*., 2000). *Cordylus giganteus* is a terrestrial cordylid that lives in colonies in burrows that individuals dig in grassland habitat (Branch, 1998). Females reproduce biennially and hibernate from May to August (Van Wyk, 1991). Offspring are born between January and April and one would expect fecundity selection to be operative in females to produce large offspring that can survive the predictable

adverse winter period when lizards are basically trapped in their underground tunnels. The situation in *C. giganteus* is thus largely comparable to that in *P. nebulosus* and *P. capensis*, but a large body of evidence is still required to come to firmer conclusions.

Like all other cordylids for which data are available, *P. nebulosus* displays male-biased dimorphism in head size. From the regression analyses of head width and head length versus SVL it is clear that both head dimensions increase at a significantly higher rate in adult males than in adult females and juveniles, possibly hinting at sexual selection for larger head sizes in males. Juvenile head length and head width were also found to increase at a significantly higher rate than that of adult females, indicating a decrease in female growth rate. According to Cooper & Vitt (1989) the most feasible explanation for this trend is that females allocate relatively more energy to reproduction after reaching sexual maturity than to characters less directly tied to reproductive success, like epidermal glands and larger head dimensions. Mouton & Van Wyk (1993) also indicated that sexual dimorphism could primarily be determined by the relative investment of females in social behaviour. As female reproduction is more energy demanding than male reproduction, differences in head size and the absence of generation glands can be ascribed to energy constraints and differential energy allocation by females (Cordes *et al*., 1995; Du Toit *et al*., 2005).

Carpenter & Ferguson (1977) found that in species where males fight, sexual selection results in an increase in the head size and also the jaw size. A larger head length results in a larger gape size and an increase in the size of the head could thus be an advantage in male-male encounters (Vitt & Cooper, 1985). Having a larger head will also reduce the energetic cost of feeding, allowing consumption of larger and harder prey items (Herrel *et al*., 2001). It seems unlikely however that natural

selection to reduce trophic competition between the sexes (Herrel *et al*., 2001) could be the causal factor for sexual dimorphism in head size in sit-and-wait foragers such as cordylids (Cooper *et al*., 1997).

Although there was a significant correlation between the increase in SVL and tail length for adult females and juveniles of *P. nebulosus*, this was not the case for males. The explanation for this could be that males with regenerated tails were also included in the analysis, as regenerated tails could easily be mistaken for intact tails in this species. The lack of difference in scar frequency between males and females may thus be misleading.

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Appendix. 2.1. Distribution of plant species through areas occupied by *Pseudocordylus nebulosus* individuals. Cover-abundance values estimated using the modified Braun-Blanquet sampling scale as in Barkman *et al*. (1964).

Landdroskop Area: 06/07/2004											
Plots	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
Distance from water	**1m**	**1m**	**0m**	**20m**	**5m**	**10m**	**30m**	**2m**	**10m**	**6m**	**20m**
Geology	TMG	TMG	TMG	TMG	TMG	TMG	TMG	TMG	TMG	TMG	TMG
Altitude	1180m	1183m	1180m	1249m	1160m	1247m	1265m	1270m	1287m	1283m	1263m
Aspect	30	110	30	75	North	North	East	East	North-east	North-east	North-east
Slope	30	45	70	75	20	45	70	50	30	50	45
Stratum 1	1.6m	0.6m	1m	0.7m	1.2m	1m	1.3m	1.5m	0.8m	0.65m	0.9m
Stratum 2	0.5m	0.2m	0.2m	0.15 m	0.65 m	0.6m	0.5m	0.3m	-	-	0.5m
% Rock cover	40	60	50	80	20	30	30	10	50	50	20
% Vegetation cover	60	40	50	20	80	70	70	90	50	50	80
GPS-S	-34º.05'	-34º.05'	-34º.05'	-34º.05'	-34º.05'	-34º.05'	-34º.05'	-34º.05'	-34º.048'	-34º.048'	-34º.04'
GPS-E	18º.99'	18º.989'	18º.99'	18º.985'	18º.99'	18º.985'	18º.985'	18º.985'	18º.9848'	18º.9847'	18º.985'
Community	Wet - Seep	Dry	Wet - Seep	Dry	Wet - Seep	Dry	Dry	Stream	Moist Slope	Moist Slope	Stream
Species											
Anthochortus crinalis (Mast.) H.P.Linder			2		2A	2A	2B		1		
Anthospermum galioides Rchb.f.				+	1	2A				+	+
Berzelia squarrosa (Thunb.) Sond.	1										
Bobartia gladiata (L.f.) Ker Gawl.		+									
Bryomorphe lycopodioides (Sch.Bip. ex Walp.) Levyns				R							
Carpacoce heteromorpha (H.Buek) L.Bolus	+										
Carpobrotus sp.										R	
Centella asiatica (L.) Urb.	1		+		+	+		+		+	
Centella eriantha (Rich.) Drude		1			+	+					
Centella triloba (Thunb.) Drude	+										
Chondropetalum deustum Rottb.		1									
Chondropetalum hookerianum (Mast.) Pillans				+							

Plots	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
Chondropetalum mucronatum (Nees) Pillans	2A							+			
Chrysithrix capensis L.	+										
Cliffortia cuneata Aiton							2A	2A			+
Cliffortia heterophylla Weim.				R							1
Clutia sp.									+		
Corymbium sp.		+		+	+	1			+	+	
Cyperaceae					R	2B	1		1	1	
Dilatris viscosa L.f.					+	+		+			
Disa racemosa L.f.			+								
Drosera sp.			1			+					
Edmondia pinifolia (Lam.) Hilliard				R							
Ehrharta sp.			3								
Ehrharta ramosa (Thunb.) Thunb.	2M				2A						
Elegia thyrsifera (Rottb.) Pers.		R		1	1				2B		
Elegia sp.1					1	+	1			1	
Elegia sp.2								3		2B	
Elytropappus glandulosus Less.				1				R	R	1	1
Erica coccinea L.								+			+
Erica hispidula L.				+						1	
Erica longifolia Aiton		+			+	1	1		2A	1	
Erica plukenetii L.		+		R	+	R			+	R	
Erica quadrangularis Salisb.							2B	+			2B
Erica sp.1	+										
Erica sp.2					R	+	+	+		+	
Erica sp.3									2A		
Erica versicolor J.C.Wendl.			+								
Erica vestita Thunb.		1		1							
Eriospermum sp.							R				
Euryops abrotanifolius (L.) DC.		R			1	+	+	1		+	
Ficinia sp.				+		+	+	+	+	+	+
Gleichenia polypodioides (L.) Sm.				R							
Gnidia oppositifolia L.			+		+			+			1
Helipterum canescens (L.) B.Nord.										+	
Hypodiscus aristatus (Thunb.) C.Krauss		+									

Plots	1	2	3	4	5	6	7	8	9	10	11
Indigofera sp.							+				
Ischyrolepis sieberi (Kunth) H.P.Linder				2A			1				
Ischyrolepis sp.											1
Leucadendron sp.					R	+	+	1		+	R
Mariscus sp.							+				
Metalasia cephalotes (Thunb.) Less.		2A			2B						
Mimetes argenteus Salisb. ex Knight											
Bryophyta			2A			+	+	+	R	+	
Osmitopsis parvifolia (DC.) Hofmeyr				R							
Osteospermum parviflora P.J.Bergius	+	R		R	R	1	+		+		+
Oxalis truncatula Jacq.								+			
Pentaschistis curvifolia (Schrad.) Stapf		+									
Pentaschistis malouensis (Steud.) Clayton		+		+		2A	1	2B	1	+	+
Penaea mucronata L.		+									
Pinus pinaster Aiton					R						
Podalyria sp.				+	2A	+					
Protea cynaroides (L.) L.							+	R		R	+
Raspalia microphylla (Thunb.) Brongn.	+		+								
Restio bifarius Mast.		R			2A	2B	R		1	2A	
Restio burchelli Pillans	+	+									
Restio corneolus Esterh.									2B		2B
Restio dispar Mast.							+	3			
Restio purpurascens Nees ex Mast.	2A	+	2								2B
Restio versatilis H.P. Linder	3	1									
Selaginella sp.			+								
Stoebe glandulosus Less.	R	1			2A	2A				R	
Tetraria capillacea (Thunb.) C.B.Clarke				2A							
Tetraria compacta Levyns	+		R	1							

Plots	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
Tetraria fasciata (Rottb.) C.B.Clarke	+	2B									
Ursinia eckloniana (Sond.) N.E.Br.	+		+				2M				
Ursinia sp.							+	+		+	+
Villarsia capensis (Houtt.) Merr.	1		1			1			R	+	
Watsonia sp.										R	R